

A MONOGRAPH OF Eucharis AND Caliphruria (AMARYLLIDACEAE)

By

ALAN W. MEEROW

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Alan W. Meerow

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By

Alan W. Meerow

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Eucharis and Caliphruria are neotropical genera of petiolate-leaved, white-flowered Amaryllidaceae found in the understory of primary tropical rainforest. Together with the Peruvian endemic Urceolina, Eucharis and Caliphruria form a monophyletic group on the basis of leaf and seed morphology and ecological specialization. Sixteen species and two natural hybrids within two subgenera are recognized in Eucharis. Subgenus Eucharis, marked by its crateriform flowers, curved perianth tube, well-developed staminal cup, and unicellular stigmatic papillae, is distributed from Guatemala to Bolivia, chiefly in the western Amazon basin and adjacent lower slopes of the eastern Andes. Subgenus Heterocharis represents three relict species with many ancestral characters of the genus. Caliphruria (4 species, 3 of which are endemic to Colombia) has funnellform flowers, straight perianth tube, reduced staminal connation, and multicellular stigmatic papillae. Abaxial leaf surfaces of both genera have dense cuticular striations. Undulate anticlinal cell walls are characteristic. A distinct palisade layer is

absent from the mesophyll. Eucharis subg. Eucharis has the least derived pollen morphology, with characteristics in common with other putatively ancestral genera of pancratioid Amaryllidaceae. Caliphruria exhibits reduction trends in pollen grain size and exine sculpturing. With the exception of two tetraploid species, all species are characterized by  $2n = 46$ . Karyomorphological change may be an important factor in species divergence. Phenetic analyses achieve only fair results in resolving phenetic relationships among Eucharis species, many of which are highly variable morphologically. Analysis of isozyme variation within two species complexes of Eucharis indicates high levels of heterozygosity. Founder effects and hybridization are respectively considered two important factors in the speciation of these groups. Modern-day distribution of Eucharis and Caliphruria is related to Pleistocene refugia theories. Phylogenetic analysis supports certain species relationships hypothesized on the basis of phenetic data, but indicates possible paraphyly for Eucharis if Caliphruria and Urceolina are segregated as a distinct genera. Acceptance of paraphyly in Eucharis is argued on the basis of degree of divergence of Caliphruria and Urceolina. The relationship between these genera is paralleled within other lineages of "infrafamily" Pancratioidinae. Keys and descriptions are provided for all species of Eucharis and Caliphruria.

## CHAPTER I INTRODUCTION

The closely-related genera Eucharis Planchon and Caliphruria Herbert (Amaryllidaceae), the Amazon lilies, comprise, respectively, 16 and 4 species of bulbous, rainforest geophytes, adapted to the low-light conditions of the forest understory. Together with the Peruvian endemic Urecolina Reichb., Eucharis and Caliphruria form a monophyletic group delimited by petiolate leaves with distinctive cuticular striation; a turgid seed with a lustrous, usually black, testa; and complete fidelity to the rainforest understory niche. The species are distributed from Guatemala to Bolivia. The major center of diversity for Eucharis is located in the western Amazon basin (inclusive of major tributary systems, e.g., the Napo, Pastaza and Huallaga) and the adjoining lower slopes of the eastern Andean cordillera. With the exception of single Peruvian species, Caliphruria is restricted to the Cordilleras Occidental and Central of Colombia. The species of both genera are nowhere abundant, and are found growing only in primary, rarely secondary, forest from ca. 50-1800 m elevation on soils of high fertility. The latter factor is probably important in limiting their distribution in the wild, and may also account for the highly localized population demographics of many of the species. Large scale deforestation has proven catastrophic to these plants. The plants are unable to adapt to the higher light intensity of the clearings and soon perish. At least several species are likely near extinction.

The Amazon lilies are marked by their evergreen, petiolate leaves; white, often pendent, sometimes fragrant flowers with a frequently conspicuous staminal cup or false corona formed by the basal connation of the staminal filaments; obtusely tri-lobed stigma; and large, turgid, ellipsoid seeds with a black, brown or metallic blue testa. A single species of Eucharis, E. amazonica Linden ex Planchon, is widely known in horticulture [erroneously as E. grandiflora Planchon and Linden (Meerow and Dehgan, 1984a)], but neither genus has never been critically treated in the taxonomic literature. Baker (1888) provided a key and descriptions for all species known at the time in his Handbook of the Amaryllideae, and Macbride (1936) treated the known Peruvian species of Eucharis for the Flora of Peru. Though species of Eucharis have continued to be described well into the present decade, the delimitation of these species from previously described taxa has consistently remained vague. No assessments of variation at either the population or species level have been attempted.

My study of these genera began in 1980. Both were combined with the closely related Urceolina by Traub (1971) without any supporting data, the investigation of which formed the basis of my unpublished master's thesis (Meerow, 1983). I refuted Traub's combination, and Eucharis was re-established as a distinct genus with three subgenera: Eucharis, Caliphruria (Herbert) Meerow ined. and Heterocharis Meerow ined. On the basis of my continuous work since that time, I now believe that Caliphruria is best retained as a distinct genus as well. This is discussed in Chapter XI. Species delimitations and associated systematic studies form the basis of this present work.



Neither Eucharis nor Caliphruria is not well represented in herbarium collections, and critical morphological characters are often obscured by the drying process. Consequently, a living collection of over 100 accessions representing one dozen species was accumulated from botanical gardens, individuals, and field collections by myself and various colleagues. Study of living material not only clarified aspects of floral and vegetative morphology, but allowed detailed study of vegetative and seed anatomy, chromosome cytology, and electrophoretic analysis of allozyme variation, as well as permitting the start of a hybridization program. Populations were observed and sampled in Colombia, Ecuador and Peru.

As two of only three genera of neotropical Amaryllidaceae (the other being the related Urceolina) exhibiting complete fidelity to a primary rainforest niche, systematic understanding of Eucharis and Caliphruria offers important information relating to the evolution of the pancratioid Amaryllidaceae ["infrafamily" Pancratioidinae sensu Traub (1963)], centered in the central Andean region of South America. As coadapted plants of the world's most complex and threatened ecosystem, their scarcity in the wild will only increase to the point of extinction if tropical deforestation continues at the present rate.

No taxonomic scheme can encompass all of the information about the group of organisms under study (Ornduff, 1969; Raven, 1976; Holsinger, 1984, 1985). In genera such as Eucharis and Caliphruria, rare in the wild and often accessible only with difficulty, and which often exhibits cryptic patterns of variation, this observation becomes that much more acute. By accumulating data from as many diverse sources as possible, I have attempted to construct a classification of the Amazon lilies that

reflects their phylogeny and inter-relationships as accurately as these data allow.



## CHAPTER II TAXONOMIC HISTORY

Herbert (1844) described the new genus Caliphruria from collections made in New Granada (Colombia) near Guaduas by Hartweg, placing Caliphruria in the "section" Pancratiformes of "suborder" Amaryllideae. Genera of this section were united by the single character of staminal connation. The small, white, funnellform flowers were marked by the presence of a bristle or slender tooth at either side of the filament. Herbert (1844) made no mention of basal connation of the filaments. The orthography of the name, a single 'l' in the Greek stem "calli-," was emended by subsequent workers (e.g. Baker, 1877), but was returned to Herbert's original by Meerow and Dehgan (1984b).

Planchon (1852) introduced another new pancratioid genus, Eucharis. The first species described, E. candida Planchon and Linden, collected in New Granada by M. Schlim, was characterized by its crateriform flowers with a conspicuous staminal cup and a widely spreading perianth limb. If Planchon was aware of Caliphruria, he did not note any relationship between it and Eucharis.

Noting the relationship between the two genera, Bentham and Hooker (1883) placed Caliphruria and Eucharis in the tribe Cyathiferae. Caliphruria subdentata Bak. was combined with Eucharis in their treatment, while C. hartwegiana Herb. was retained. Baker (1888) accepted this treatment, and described another new species as C. tenera. He described Caliphruria as "nearly allied to Eucharis."

Baillon (1894) described the species C. castelnaeana and declared it precisely intermediate between Caliphruria and Eucharis. He further suggested that Eucharis should be treated as a section of Caliphruria. Macbride (1931) later transferred C. castelnaeana to Eucharis.

Nicholson (1884) transferred C. hartwegiana (the type species of Caliphruria) to Eucharis, ignoring the fact of the former's nomenclatural priority. Traub (1967) made the formal transfer of the remaining species of Caliphruria, C. tenera Baker, to Eucharis and also combined the monotypic genus Plagiolirion Baker (1883) with Eucharis. He had previously listed Caliphruria, Plagiolirion, and Mathieua Klotzsch [another monotypic genus (Meerow, MS in subm.)] as synonyms for Eucharis in his Genera of the Amaryllidaceae, citing Baillon (1894) as a "special reference" (Traub 1963, p. 74). The nomenclatural priority of Caliphruria Herbert was overlooked. No proposal for the conservation of Eucharis Planchon over Caliphruria Herbert has ever been proposed previous to that of Meerow and Dehgan (1984b).

Traub (1971) later combined Eucharis with Urceolina Reich. (nom. cons.), a small Andean genus with petiolate leaves and markedly urceolate, brightly colored flowers. He designated five subgenera: Urceolina, Eucharis, Caliphruria, Mathieua, and Plagiolirion. Traub (1971) offered no explanation for the combination of Eucharis and Urceolina, but presumably his decision was prompted in part by reports in the literature of two intergeneric hybrids between Eucharis and Urceolina: X Urceocharis clibranii Masters, an artificial hybrid, and X U. edentata C. H. Wright, putatively discovered in the wild state in Peru.

In my preliminary work (Meerow, 1983; Meerow and Dehgan, 1984a, b), I refuted Traub's unsupported combination, re-establishing Eucharis (including Caliphruria), Plagiolirion, and Mathiuea as distinct genera. Plagiolirion and Mathiuea are monotypic genera allied to Hymenocallis Salisb. and Stenomesson Herbert respectively (Meerow, MS in subm.). On the basis of the work detailed in the following chapters, I prefer to treat Caliphruria as a distinct genus as well.

## CHAPTER III VEGETATIVE MORPHOLOGY

### Materials and Methods

#### Leaf Surface Morphology [Scanning Electron Microscopy (SEM)]

Fresh material was fixed in FAA for a minimum of 24 hrs. Leaf sections were always taken from midpoint of the lamina. Samples were EtOH-dehydrated, critically point dried with a Denton DCP-1 apparatus, mounted, and coated with 600 Å of gold-palladium mixture with a Technics Hummer V sputter coater. Specimens were observed and photographed on an Hitachi S-450 scanning electron microscope at 20 kv.

#### Anatomical Studies

Petioles were freehand sectioned with teflon coated razor blades, and lightly stained with toluidine blue. Leaf clearings were prepared by immersing fresh, medial lamina sections in 85% lactic acid at 45° C for 5-7 days. Abaxial and adaxial epidermal layers were then separated using diluted Jeffrey's (1917) solution. Epidermal tissue was stained in 1% safranin, and mounted in 1:1 glycerol - 95% EtOH mixture. Leaf tissue (medial lamina) fixed in FAA was processed for paraffin block sectioning with an American Optical T/P 8000 tissue processor. Dehydration began with 50% EtOH, and continued through 50-100% tert-butyl alcohol. Dehydrated material was then transferred to a 1% solution of safranin, followed by a 1:1 mixture of absolute tert-butyl alcohol

and mineral oil, a 3:1 mixture of Paraplast and mineral oil, and finally 100% Paraplast. Embedded material was sectioned with an American Optical No. 820 rotary microtome set at 10  $\mu$ m. Sections were further stained with toluidine blue. Sections were mounted using Pro-Texx mounting medium. All material was examined and photographed on a Nikon Labophot photomicroscope with AFX-II photographic attachment. Terminology is referable to Stace (1965) and Dilcher (1973).

### Statistical Procedures

Statistical tests were performed with SAS Release 5.08 (SAS Institute, INC.) on the Northeast Regional Data Center (NERDC) of the University of Florida.

## Results and Discussion

### Bulbs

The globose or subglobose bulbs of Eucharis and Caliphruria, composed of concentric and modified leaf bases (scales), are characteristic of most members of the Amaryllidaceae. The outer scales of Eucharis and Caliphruria bulbs are modified into a papery tunic, either brown or tan in color. On the whole, little systematic information can be derived from bulb morphology. Size of mature bulbs is variable and proportional to the whole plant size range of each species.

The bulb scales of most species of Eucharis and Caliphruria are apically articulated into a neck or pseudostem of variable length. Distally, the pseudostem grades into the petiole of individual leaves.

Unlike species of Hymenocallis subg. Ismene, the neck of Eucharis and Caliphruria bulbs always remains below the soil surface. Length of the neck may therefore be more a factor of bulb depth in the substrate rather than of any phylogenetic significance.

Van Bragt et al. (1985) found flower initiation will not occur in bulbs of E. amazonica less than 35 mm diameter. This species characteristically produces among the largest bulbs of any in the genus.

Irmisch (1850) recognized the existence of both monopodial and sympodial shoot structure in bulbs of Amaryllidaceae. Pax (1888) and Troll (1937) followed these same concepts, but other workers, (e.g. Church, 1919; Peter, 1971; Brunard and Tulier, 1971; U. and D. Müller-Doblies (1978), Dzidziguri, 1978; Akensova and Sedovi, 1981; and Arroyo, 1984) have not always been in agreement as to which shoot structure was applicable to various taxa. Most recently, Arroyo (1984) characterized only four South African taxa as possessing true monopodial organization. She is now in accord (Arroyo, pers. comm.) with Müller-Doblies and Müller-Doblies (1972) who suggest that only sympodial structure occurs in bulbs of Amaryllidaceae.

Bulbs of Eucharis and Caliphruria are, without controversy, true sympodia (Arroyo, 1984; van Bragt et al., 1985). Each bulb has a single terminal vegetative meristem. After its transformation to a floral apex, a new vegetative growing point is formed laterally.

Bulbs of most species of Eucharis and Caliphruria offset regularly and vigorously, forming sizable clumps in time if undisturbed. Offset bulbs are at first usually tightly joined at the basal plate to the parent bulb. Only very rarely does an elongated rhizome develop from which a new shoot system can arise at some distance from the parent



plant, a mode of vegetative reproduction characteristic of some species of Hymenocallis (pers. obs.; T. Howard, pers. com.).

### Leaf Gross Morphology

Leaves of Eucharis and Caliphruria are uniformly long-petiolate, with a well-developed elliptic, ovate or lanceolate lamina. Petiolate leaves are characteristic of a number of genera of Amaryllidaceae, either completely or in part, and have undoubtedly evolved independently several times from the linear or lorate leaf morphology typical of the family. In most of these cases, the petiolate leaf appears to be primarily an adaptation to reduced levels of light concurrent with colonization of forest understory (e.g. Eucharis, Caliphruria, Urceolina, Eurycles Salisb., Scadoxus (Raj.) F. Nardal, Hymenocallis tubiflora Salisb. and allied species.). Foilage of petiolate-leaved genera occurring in more open situations (e.g. Phaedranassa Herbert, Rauhia Traub), is generally marked by increased succulence and/or pruinosity [leaf surface wax is capable of reflecting light and heat (Cutler et al., 1980)].

The petiole of the leaf of Eucharis and Caliphruria is usually as long or longer than the lamina. It is subterete in cross-section (Fig. 1-2), rounded abaxially, and flattened adaxially, becoming slightly channelled proximal to the sinus. The petiole is winged proximal to the sinus by the attenuation of the lamina. The midrib is pronounced abaxially along the entire length of the lamina, and slightly channelled adaxially, continuous with the petiole.

Leaf shape only rarely provides taxonomically useful information. Length : width ratios are subject to considerable variation even among

the leaves of a single bulb. Herbarium specimens will frequently include only a single leaf, with no indication of its developmental age. Taxonomic consistency of leaf shape is exceptional, but useful in the few cases where it occurs. For example, leaves of E. ulei are consistently narrowly elliptic. Eucharis amazonica (leaf length/width ratio greater than 2) may be delimited from E. anomala (l : w less than 2).

The leaves of Eucharis and Caliphruria are completely glabrous and non-glaucous with a single exception. Eucharis bonplandii (Kunth) Traub, a rare tetraploid species from central Colombia, develops a glaucous bloom in strong light that gives the leaf a blue cast.

The leaves of Caliphruria are slightly thicker than those of subg. Eucharis and Heterocharis. This may reflect adaptation to slight water stress, as the species of Caliphruria sometimes inhabit slightly drier forest associations than characteristic of the Eucharis (see Chapter IX). Eucharis bouchei Woodson and Allen and E. bonplandii (both subg. Eucharis), however, have thickened leaves, possibly a consequence of their tetraploid constitution (see Stebbins, 1950).

The leaf apex of all species is shortly acuminate, the base attenuate. Coarse undulation of the margin will sometimes make the lamina appear cordate at the base. Leaf margins of Caliphruria are uniformly non-undulate.

Venation of the leaf of Eucharis and Caliphruria is parallelodromous (Hickey, 1973), with a great number of transverse, commissural veins inter-connecting the primary vasculature. Whether the leaf is plicate along the primary veins can be a taxonomically useful character. Unfortunately, this, and many other leaf characters (e.g.,



marginal undulation, the color and luster of the epidermis), readily observed in live material, are completely obscured in herbarium specimens.

All species of Caliphruria have smooth, non-plicate leaves. Eucharis is variable for this character, but the majority of species of have plicate leaves.

The adaxial epidermis of most species of both genera is a lustrous, dark green; the abaxial surface appears lighter, or silvery-green. Only E. astrophiala (Ravenna) Ravenna has diverged markedly from the typical morphology, and has a uniquely non-lustrous, bullate-pustulate leaf texture.

#### Leaf Surface Features

Cuticle. Cuticular striation is prominent on the abaxial leaf surfaces of most Eucharis and Caliphruria species (Fig. 3-7, 9-13, 15-18). Striae are thickest in C. subedentata (Fig. 6). Arroyo and Cutler (1984) recognized eight cuticular sculpturing classes in a survey of 25 genera of Amaryllidaceae. The most common cuticular morphology of Eucharis and Caliphruria fits their class VII: "thick striae, parallel or not, interlocking, + transverse" (Arroyo and Cutler, 1984, p. 471), a type they reported only for the few species of Phaedranassa, Scadoxus, and Griffinia Ker-Gawl. that they examined, all three genera with petiolate leaves, but not closely related. Phaedranassa is, however, rather variable in its cuticular morphology (Meerow, unpubl.). Eucrosia Ker-Gawl., a close ally of Phaedranassa, also has cuticular striation similar to that of Arroyo and Cutler's type VII (Meerow and Dehgan, 1985), but differs in the orientation, thickness and pattern of the

striae. Urceolina, a small genus very closely related to Eucharis and Caliphruria, has cuticular morphology much like that of the latter genera.

In a few species of Eucharis (E. amazonica, E. anomala (Fig. 3; E. bouchei, Fig. 18) the striation is much less pronounced. Caliphruria korsakoffii (the sole representative of Caliphruria outside Colombia) has the most aberrant cuticle morphology (Fig. 7), corresponding more or less to type V of Arroyo and Cutler (1984): "central, thick axial striation with less pronounced striae running from it, directly to anticlinal walls" (Arroyo and Cutler, 1984, p. 471). The adaxial cuticle of Eucharis and Caliphruria is either smooth or rarely much more finely striate than the abaxial surface, the striations entirely axial. The adaxial cuticle of C. korsakoffii (Fig. 8) has several, thick, transverse striations across each cell, and the epidermis is unusually flat in topography.

Stomata. Leaves of Eucharis and Caliphruria are predominantly hypostomatic. Stomata occur adaxially only along the midrib and vicinity (Fig. 19A), and also occasionally in the proximity of primary veins. Stomata are usually absent from the abaxial midrib (Fig. 19B). Intercalary stomata were regularly observed only in E. cyaneosperma Meerow (Fig. 14 & 21C). A survey of leaf surfaces in "infrafamily" Pancratioidinae (Meerow, unpubl.) suggests that loss or reduction of adaxial stomata frequently accompanies the evolution of petiolate leaves in Amaryllidaceae. Most linear or lorate-leaved genera are amphistomatic. The stomata of Eucharis and Caliphruria are anomocytic, as is typical for Amaryllidaceae (Arroyo and Cutler, 1984; Dahlgren and Clifford, 1982), though E. astrophiala exhibits at least slight

differentiation of cells neighboring the stomata (Fig. 9-10) from other epidermal cells. These cells are more densely and regularly striate than other epidermal cells, as well as slightly more upraised. The guard cells of Eucharis and Caliphruria are oriented with their longest axis parallel to that of the leaf. Wide variation in stomatal index  $\{[\text{no. of stomata} / (\text{no. of stomata} + \text{no. of epidermal cells})] \times 100$  (Salisbury, 1927)} is evident (Table 2). Intraspecific variation in SI can be as wide as that between species, however, and seems to have little taxonomic significance. Correlations between SI and leaf width, length and length:width ratios were tested for all plants examined. Pearson correlation coefficients for the three comparisons were 0.249 (width), 0.421 (length) and 0.232 (length:width). Greatest correlation of SI was with leaf length, but none of the three tested factors are very significant. Salisbury (1927) reported that humidity affects stomatal index, and other workers (Yapp, 1912; Gupta, 1961) have suggested that SI may not be as invariant as has been claimed. The great morphological variation of Eucharis species (subg. Eucharis in particular) in characters of floral morphology (Chapter IV) is also present in vegetative characters.

Epidermal cells. The epidermal cells of all species of E. subg. Eucharis have strongly undulate anticlinal walls (Fig. 20-23A), as noted by Asatrian (1984) for the few species he surveyed. Abaxial cells are more strongly undulate than those of the adaxial surface. Abaxial epidermal cells of Caliphruria (Fig. B-C) are more weakly undulate, and the adaxial cells of C. korsakoffii (Fig. 24C) are completely straight. Eucharis subg. Heterocharis is polymorphic for anticlinal wall morphology. Eucharis amazonica (Fig. 23A) and E.

sanderi (not illustrated) have strongly undulate walls, while E. anomala (Fig. 23B) has essentially straight walls. I have surveyed the leaf surface morphology of all genera in "infrafamily" Pancratioidinae with the exception of Pucara Ravenna (Meerow, unpubl.). Strongly undulate anticlinal walls are very rare among these genera. Arroyo and Cutler (1984) report similar findings for the genera of pancratioid Amaryllidaceae that they surveyed. Arroyo and Cutler (1984) and Artushenko (1980) consider undulate anticlinal walls to be primitive for the family. No detailed reasons are given by these authors for this assessment, though reference is made to Scadoxus, a putatively primitive bulbless genus of African Amaryllidaceae with undulate anticlinal walls and Type VIII striation. This genus is often considered close to the ancestral complex that gave rise to the Amaryllidaceae (Arroyo, 1982; Arroyo and Cutler, 1984; Nordal and Duncan, 1984). Yet Scadoxus has a baccate fruit, "brush" type inflorescence morphology, and petiolate leaves (Nordal and Duncan, 1984), all derived characters in relation to the rest of the family (Meerow, 1985a). Consequently, there seems little evidence to suggest that the undulate anticlinal walls of Scadoxus represent the primitive condition for the Amaryllidaceae. Eucharis anomala, putatively the most primitive species of Eucharis (see Chapter XI) has straight anticlinal walls (Fig. 23B). Taking this fact into consideration, along with the relative rarity of undulate anticlinal walls throughout the Pancratioidinae, I believe the undulate condition is more likely the derived state. End walls of the both the abaxial and adaxial cells of all species range from oblique to rounded.

Abaxial epidermal cells range from rectangular to irregular in shape. Adaxial epidermal cells are, in almost all cases, rectangular.

Eucharis astrophiala (Fig. 20A) has the most irregularly shaped cells of both the abaxial and adaxial surfaces. In the vicinity of the midrib on both surfaces of the leaf (Fig. 19), epidermal cells become conspicuously elongated, and anticlinal walls are straight. Epidermal cells of the midrib are extremely long and narrow.

#### Leaf Anatomy

In petiolar transverse section, a single arc of vascular bundles is usually observed (Fig. 1-2). Median bundles are the largest. In petioles of E. anomala Meerow (Fig. 2B) and the closely related E. amazonica (Fig. 2C), both in subg. Heterocharis, small secondary bundles were observed near the adaxial surface. These bundles are most conspicuous in E. anomala; they are markedly smaller in E. amazonica. These secondary vascular traces disappear above the middle of the petiole. Asatrian (1984), who reported on petiole anatomy of three Eucharis and Caliphruria species, did not observe these bundles in E. amazonica (cited as E. grandiflora).

The internal morphology of leaves of Eucharis and Caliphruria (Fig. 25-31) is largely invariant across both genus. No well defined palisade layer is evident, a characteristic of most genera of "infrafamily" Pancratioidinae (Arroyo and Cutler, 1984; Meerow, unpubl. data). Mucilage cells, common throughout the family (Arroyo and Cutler, 1984), are often present near the leaf surface, and raphides are occasionally observed in epidermal cells. The mesophyll consists of several layers of chlorenchyma both ad- and abaxially, and a thicker region of spongy, slightly aerenchymous tissue. Small air cavities occur regularly only directly below stomata. Vascular bundles are

surrounded by a sheath of 1-2 layers of parenchymous cells. The only xylem elements present are tracheids with annular thickenings (Fig. 28).



Table 3.1. Leaf length, width, length : width ratio, and stomatal index of *Eucharis* and *Caliphruria* species. All voucher specimens are deposited at FLAS unless otherwise indicated.

TAXON	VOUCHER	LEAF LENGTH (cm)	LEAF WIDTH (cm)	L : W	STOMATAL INDEX
<i>Eucharis</i> subg. <i>Eucharis</i>					
<i>E. astrophiala</i>	Meerow 1140	19.0	8.0	2.38	10.42
<i>E. bonplandii</i>	Bauml 686 (HUNT)	17.5	8.5	2.06	12.70
<i>E. bouchei</i> var. <i>bouchei</i>	Meerow 1125	24.0	8.5	2.82	14.74
<i>E. bouchei</i> var. <i>dressleri</i>	Meerow 1107	24.0	10.0	2.40	11.61
<i>E. candida</i>	Meerow 1144	27.0	9.0	3.00	24.79
	Schunke 14155-B	32.5	9.1	3.57	15.72
<i>E. castelnaeana</i>	Schunke 14156	17.5	7.0	2.50	9.33
<i>E. cyaneosperma</i>	Meerow 1032	31.5	7.5	2.36	17.21
<i>E. formosa</i>	Meerow 1099	51.0	15.0	3.40	18.18
	Meerow 1103	35.0	10.0	3.50	16.34
	Schunke 14157	35.0	10.5	3.33	14.45

Table 3.1--continued.

TAXON	VOUCHER	LEAF LENGTH (cm)	LEAF WIDTH (cm)	L : W	STOMATAL INDEX
	<u>Schunke 14171</u>	37.5	15.0	2.50	18.57
	<u>Schunke 14174</u>	42.0	14.8	2.94	12.95
<u>E. plicata</u> subsp. <u>plicata</u>	<u>Meerow 1025</u>	26.0	12.0	2.17	9.92
<u>E. plicata</u> subsp. <u>brevidentata</u>	<u>Meerow 1143</u>	19.5	10.0	1.95	20.79
<u>Eucharis</u> subg. <u>Heterocharis</u>					
<u>E. amazonica</u>	<u>Schunke 14179</u>	35.0.	13.5	2.59	12.29
<u>E. anomala</u>	<u>Meerow 1141</u>	22.5	12.5	1.89	12.36
X <u>Calicharis</u> <u>butcheri</u>	<u>Meerow 1110</u>	22.0	10.5	2.10	16.01
<u>E. X grandiflora</u>	<u>Meerow 1127</u>	27.0	14.5	1.86	14.00



Table 3.1--continued.

TAXON	VOUCHER	LEAF LENGTH (cm)	LEAF WIDTH (cm)	L : W	STOMATAL INDEX
<u>Caliphurria</u>					
<u>C. korsakoffii</u>	<u>Meerow 1096</u>	13.5	3.8	3.55	10.15
<u>C. subdentata</u>	<u>Meerow 1109</u>	16.8	6.8	2.47	14.21
	<u>Meerow 1123</u>	16.5	8.0	2.06	9.36
	<u>Meerow 1159</u>	15.7	7.5	2.09	10.11

Pearson correlation coefficients (significance is indicated by proximity of value to 1):

Stomatal index and leaf length = 0.421

Stomatal index and leaf width = 0.249

Stomatal index and leaf length/width ratios = 0.232

Figure 3.1. Petiole transverse sections of Eucharis species. A. E. astrophiala (Madison 3792, SEL).  
B. E. bouchei var. dressleri (Meerow 1108, FLAS). C. E. plicata subsp. plicata (Meerow 1025,  
FLAS). p = proximal, m = medial, d = distal.

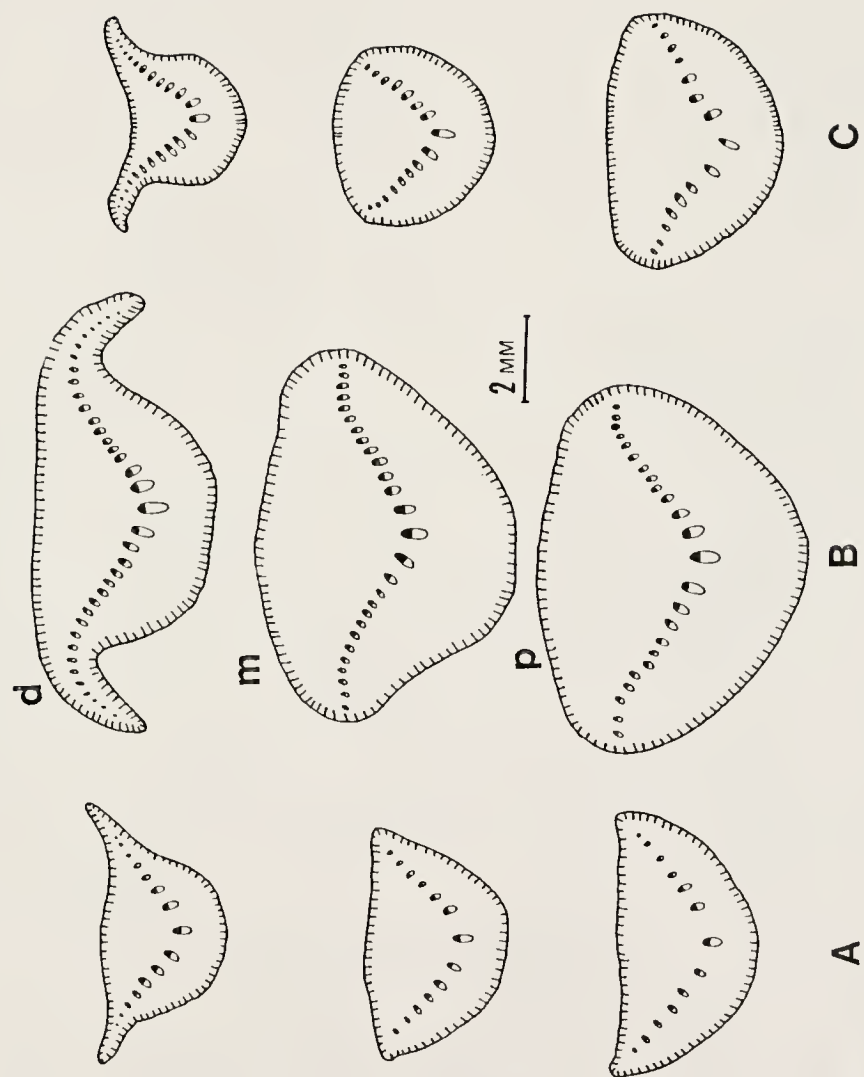
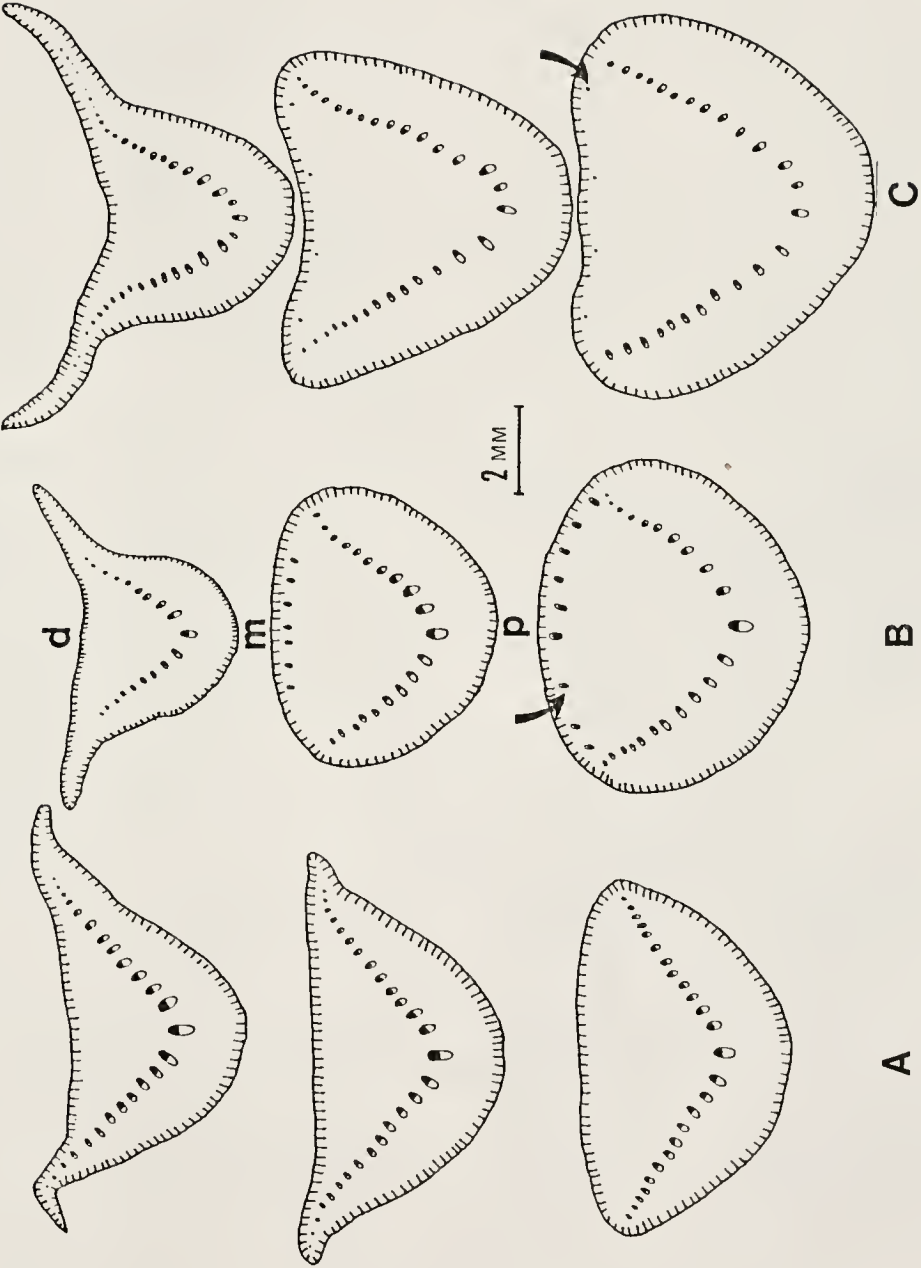
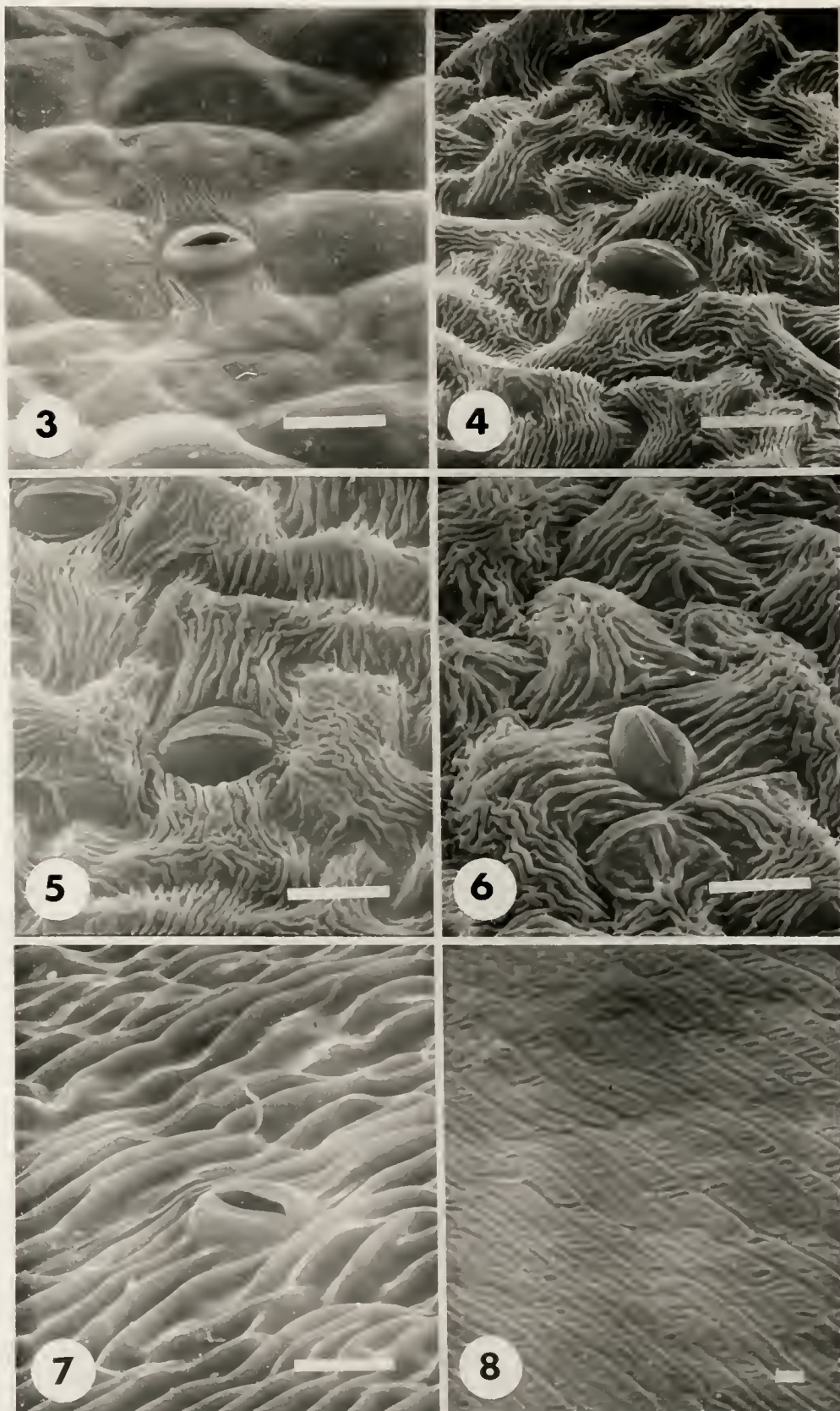


Figure 3.2. Petiole transverse sections of *Eucharis* and *Caliphruria* species. A. *C. subdentata* (Meerow 1156, FLAS). B. *E. anomala* (Meerow 1141, FLAS). C. *E. amazonica* (Schunke 14179, FLAS).  
p = proximal, m = medial, d = distal.



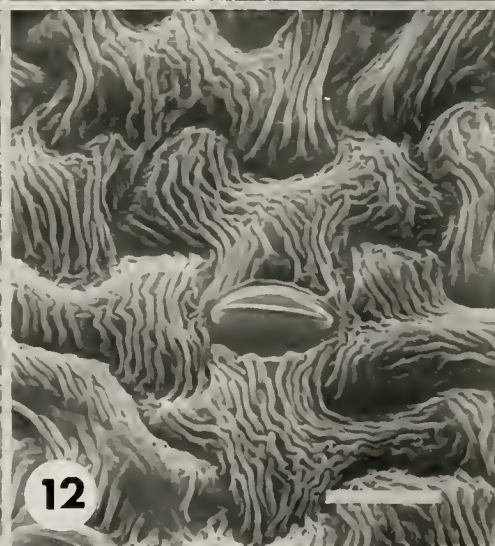
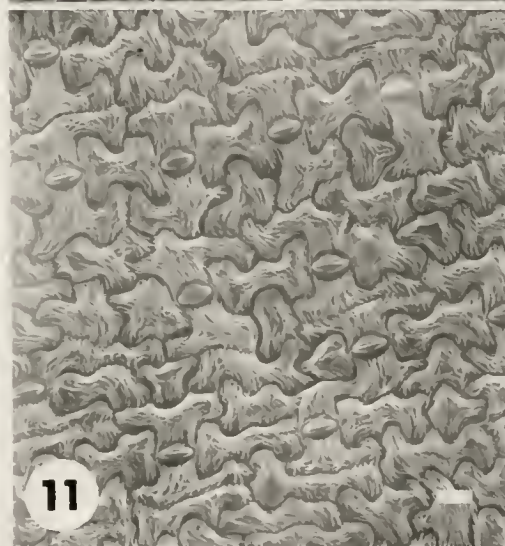
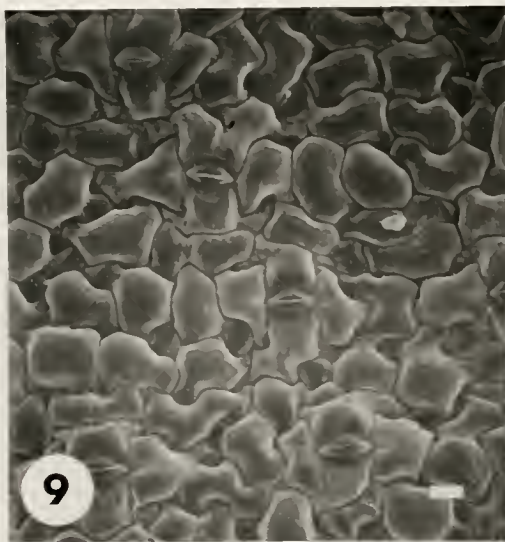
Figures 3.3-3.8. SEM photomicrographs of Eucharis and Caliphruria leaf surfaces. 3-7. Abaxial surfaces. 3. E. anomala (Meerow 1141, FLAS). 4. E. X grandiflora (Madison et al. s. n., SEL). 5. X Calicharis Butcheri (Meerow 1110, FLAS). 6. C. subdentata (Meerow 1109, FLAS). 7. C. korsakoffii (Meerow 1096, FLAS). 8. Adaxial surface of C. korsakoffii (Meerow 1096, FLAS). All scales = 25  $\mu$ m.





Figures 3.9-3.14. SEM photomicrographs of Eucharis leaf surfaces. 9-13. Abaxial leaf surfaces. 9-10. E. astrophiala (Meerow 1111, FLAS). 11-12. E. plicata subsp. plicata (Meerow 1025, FLAS). 13. E. cyaneosperma (Meerow 1032, FLAS). 14. Adaxial leaf surface, E. cyaneosperma (Meerow 1032, FLAS). All scales = 25  $\mu$ m.





Figures 3.15-3.18. SEM photomicrographs of Eucharis abaxial leaf  
surfaces. 15. E. bakeriana (Meerow 1108, FLAS). 16. E. formosa  
(Meerow 1103, FLAS). 17. E. bonplandii (Bauml 686, HUNT). 18.  
E. bouchei var. dressleri (Meerow 1107, FLAS). All scales = 25  
µm.

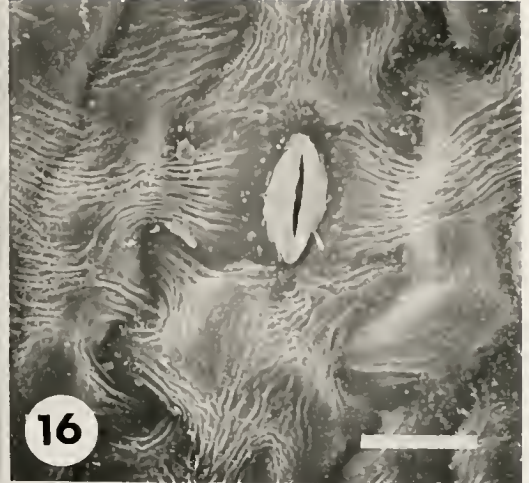
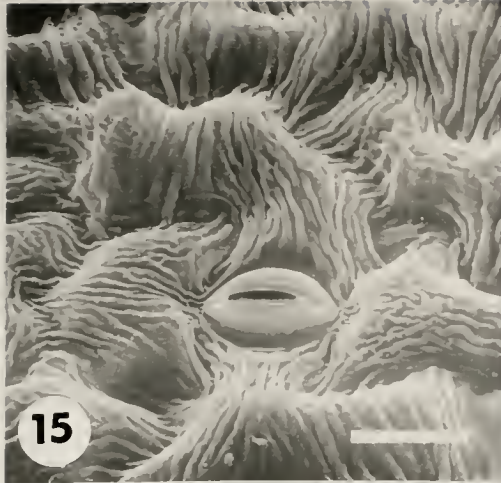
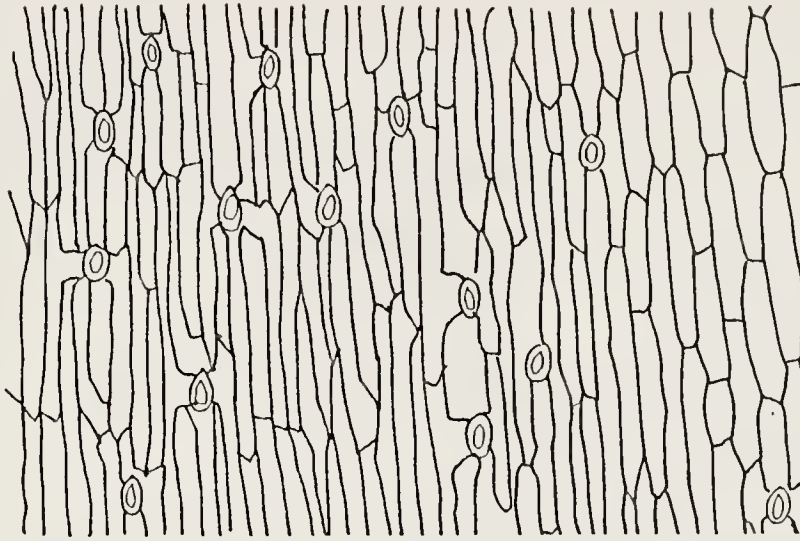


Figure 3.19. Leaf epidermal cell configurations of representative Eucharis species in the vicinity of the midrib. A. E. formosa (Schunke 14174, FLAS), adaxial surface. B. E. plicata subsp. plicata (Meerow 1025, FLAS).



**A**

0.2 mm

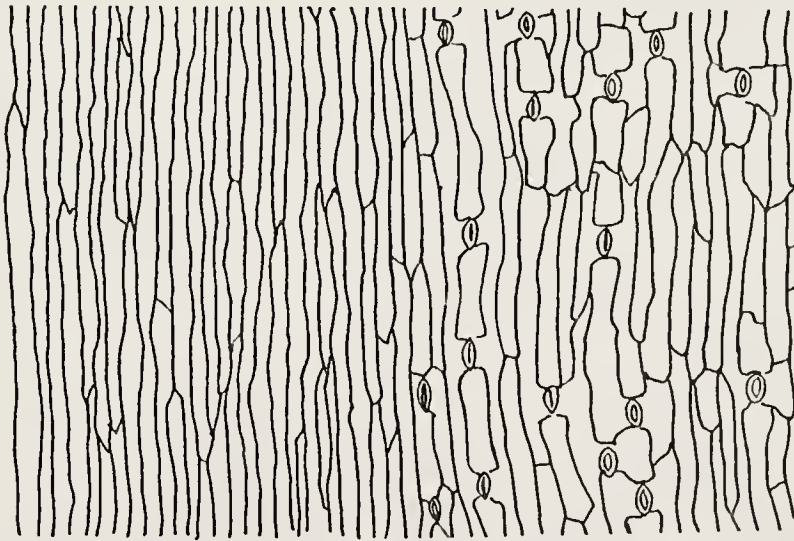
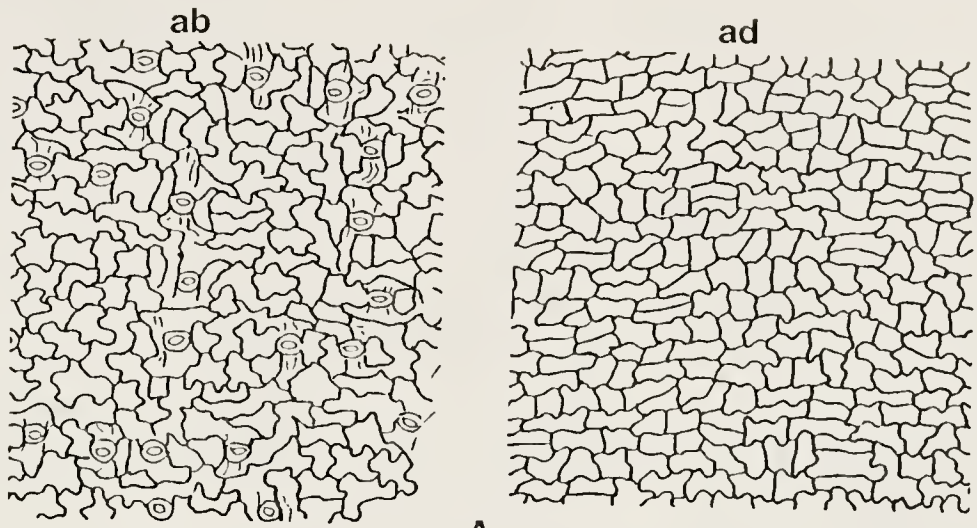
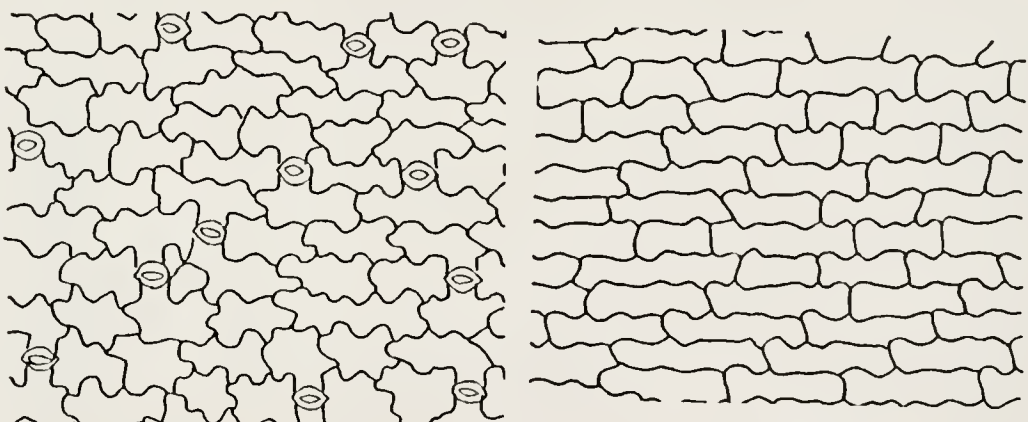
**B**

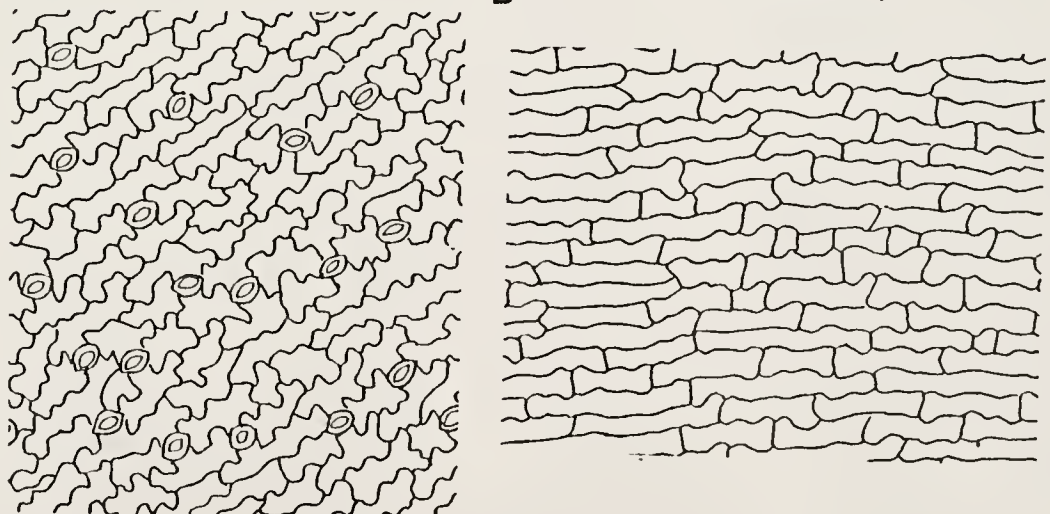
Figure 3.20. Leaf epidermal configurations of Eucharis species in the inter-costal area of the leaf. A. E. astrophiala (Madison 3792, SEL). B. E. bonplandii (Bauml 686, HUNT). C. E. bouchei var. bouchei (Meerow 1125, FLAS).



A



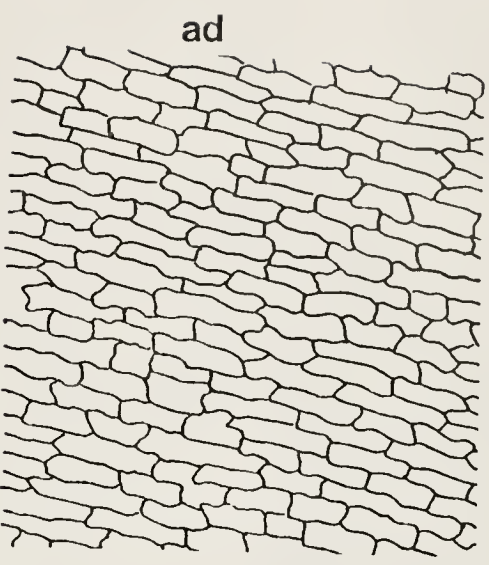
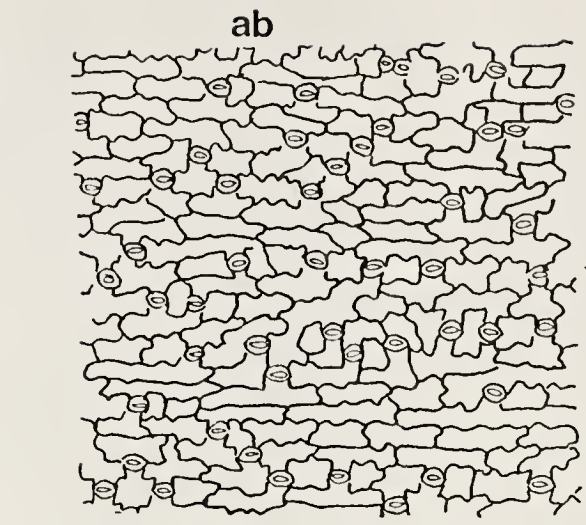
B



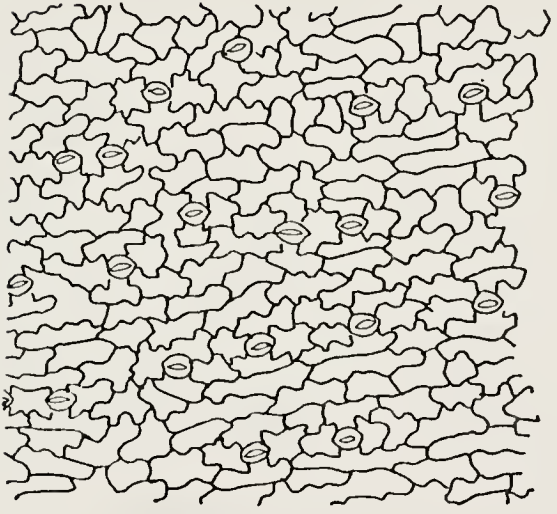
C



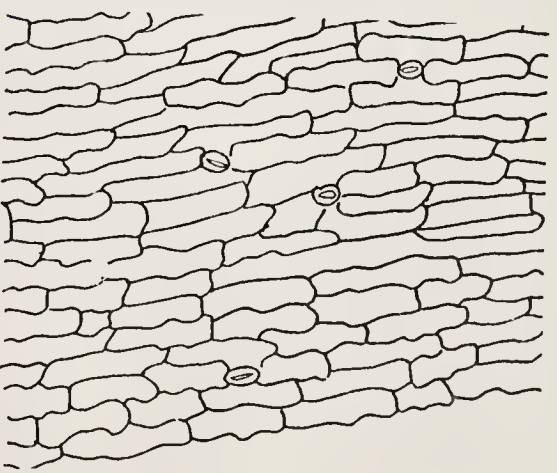
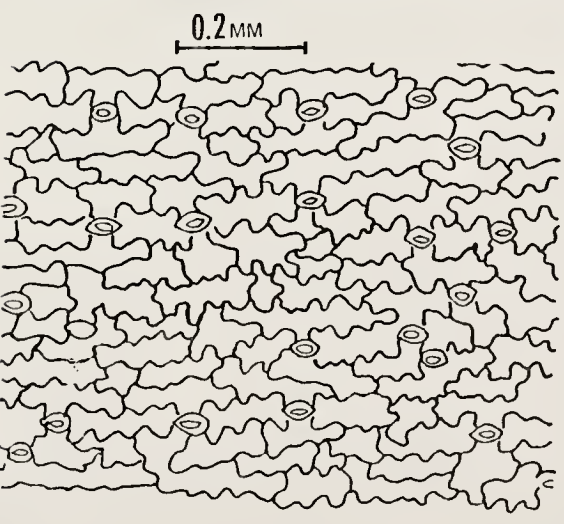
Figure 3.21. Leaf epidermal configurations of Eucharis species in the inter-costal area of the leaf. A. E. candida (Meerow 1144, FLAS). B. E. castelnaeana (Schunke 14156, FLAS). C. E. cyaneosperma (Meerow 1032, FLAS).



A

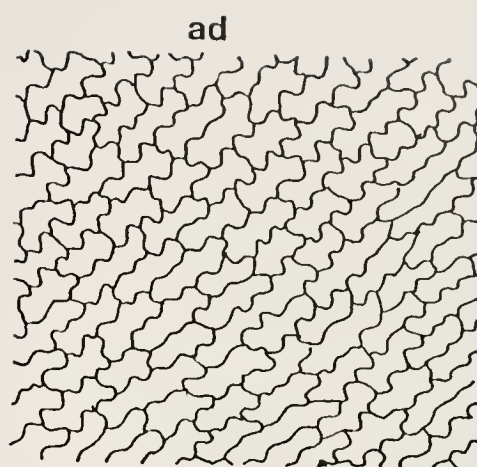
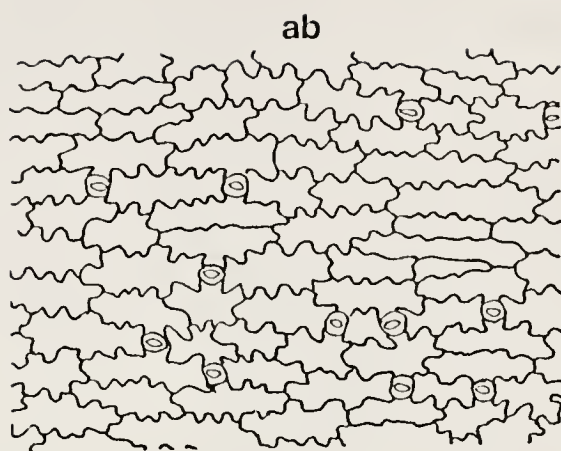


B

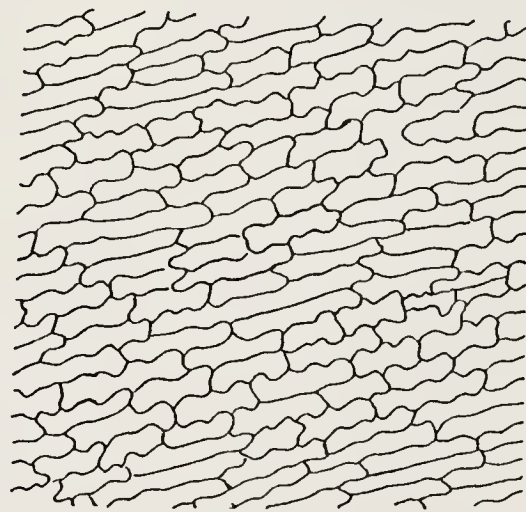
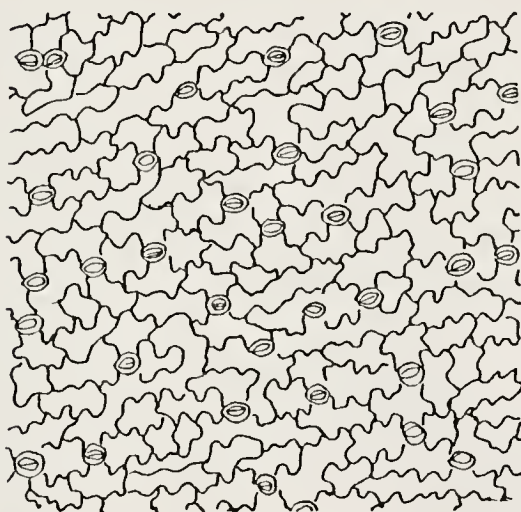


C

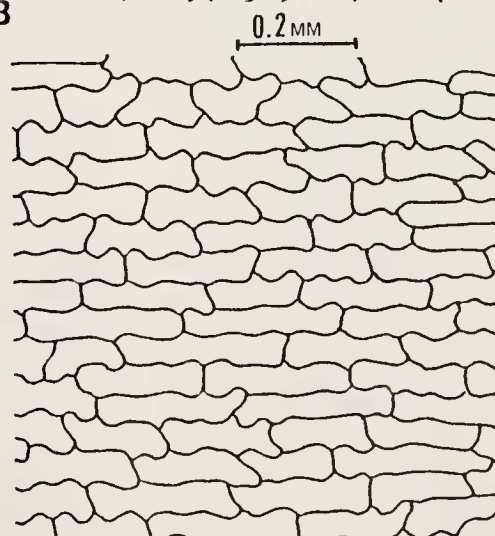
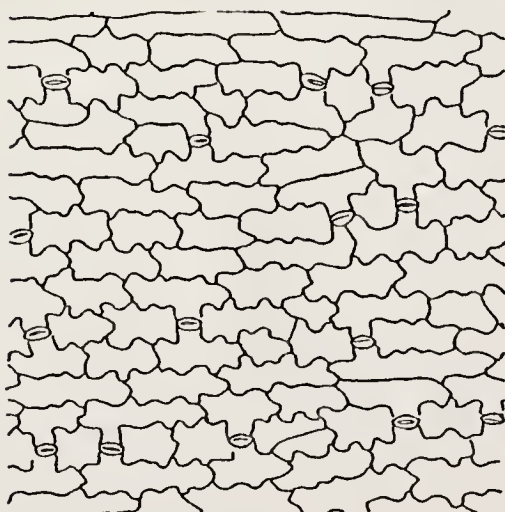
Figure 3.22. Leaf epidermal configurations of Eucharis species in the inter-costal area of the leaf. A. E. formosa (Schunke 14174, FLAS). B. E. plicata subsp. brevidentata (Meerow 1143, FLAS). C. E. ulei (Schunke 14153, FLAS).



A



B



C

Figure 3.23. Leaf epidermal configurations of Eucharis species in the inter-costal area of the leaf. A. E. amazonica (Schunke 14179, FLAS). B. E. anomala (Meerow 1141). C. E. X grandiflora (Meerow 1127, FLAS).

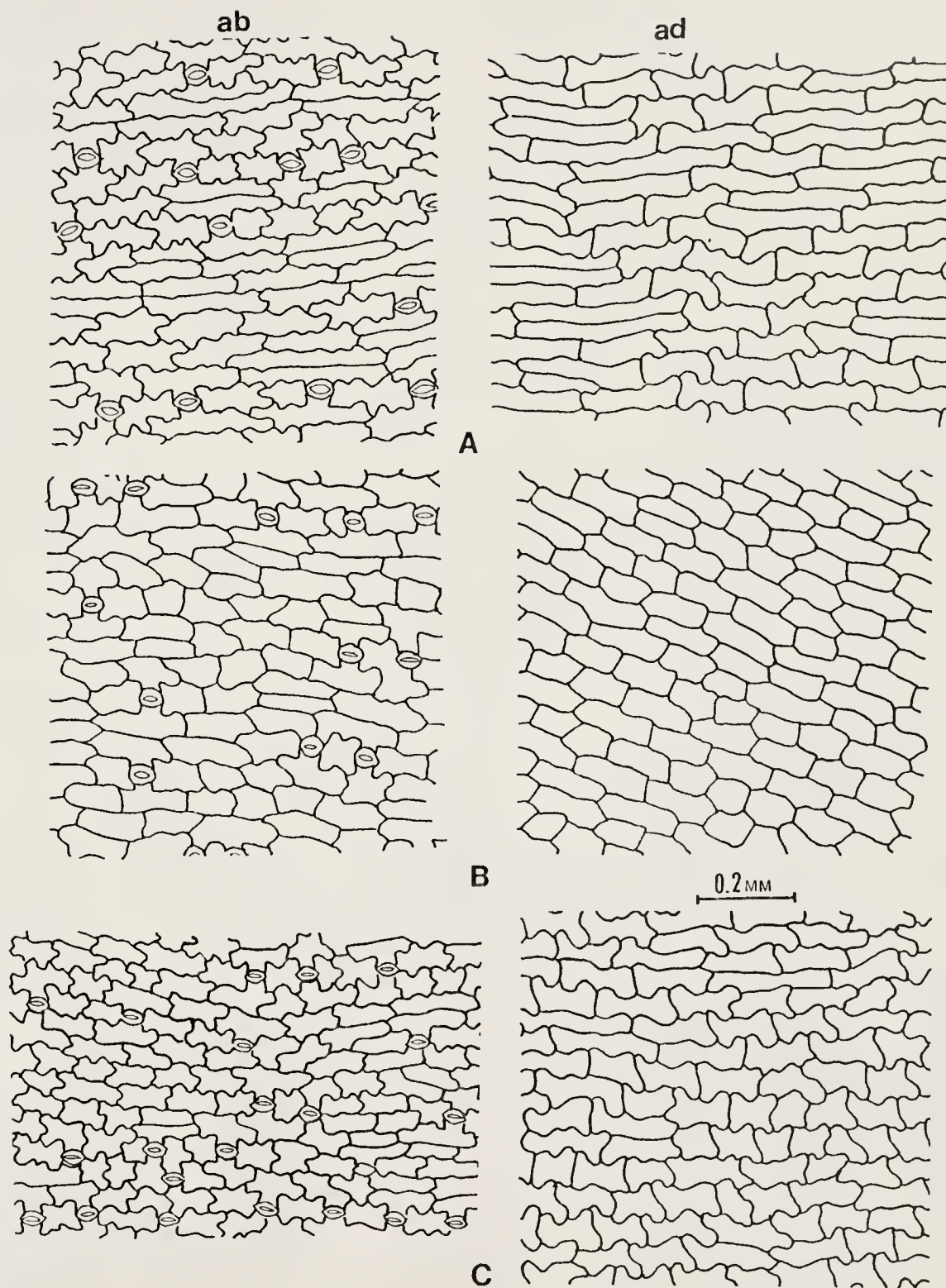
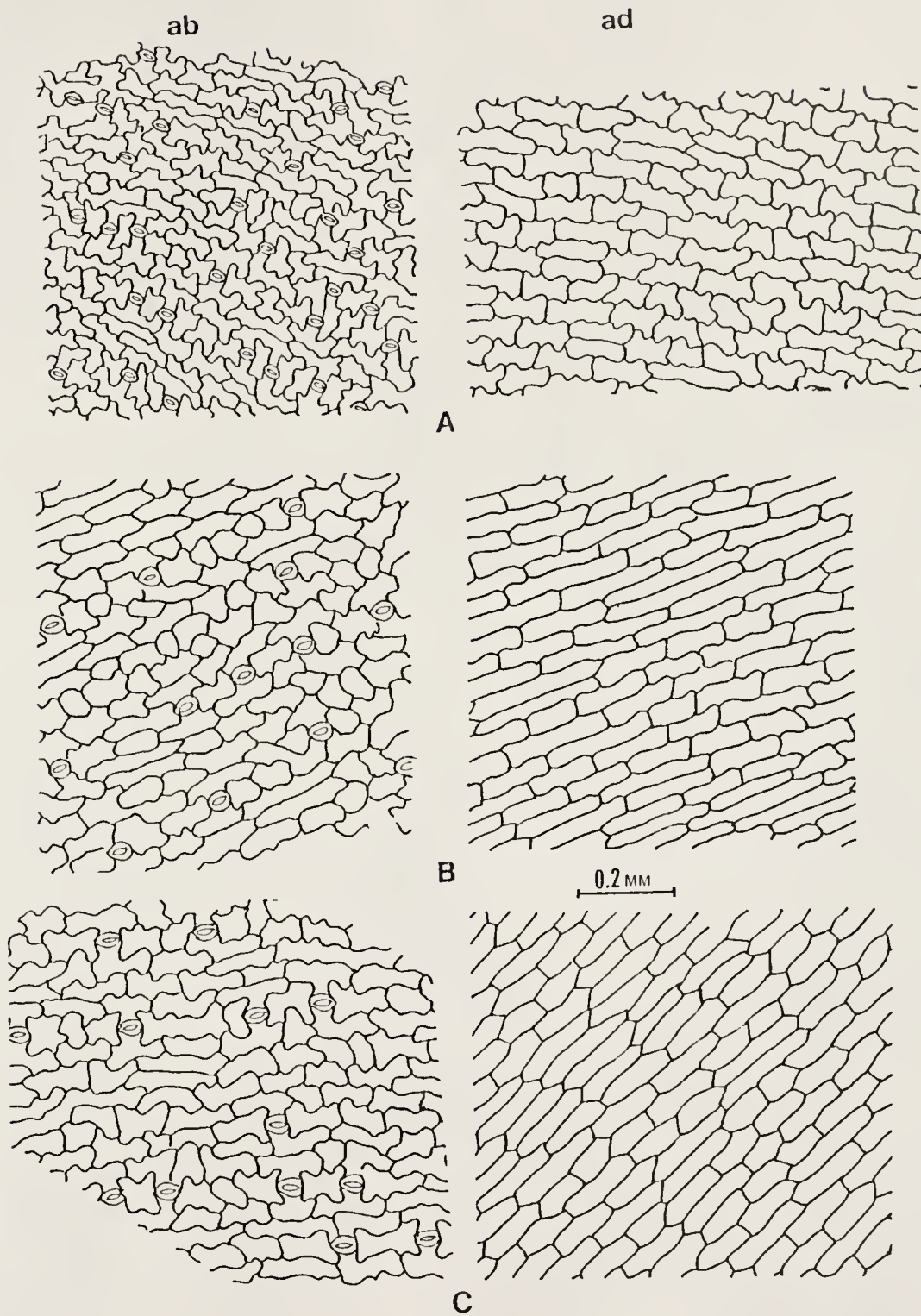


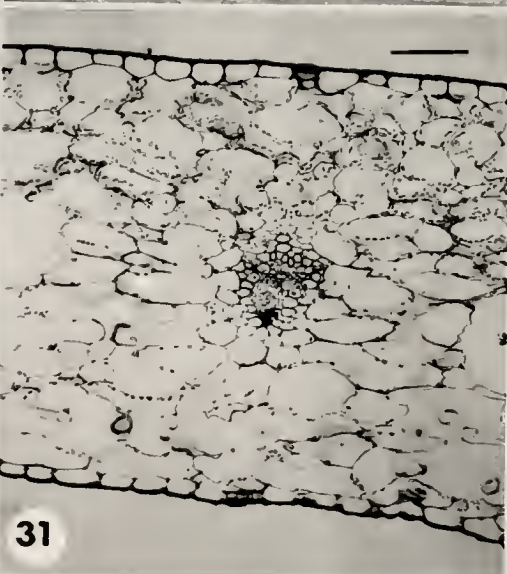
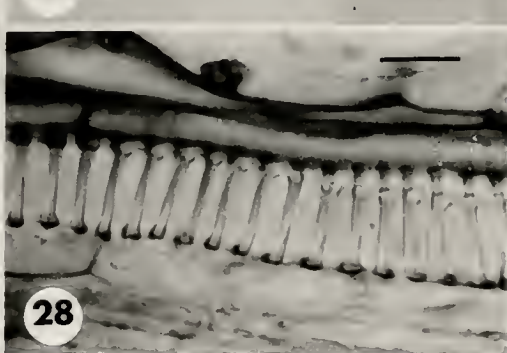
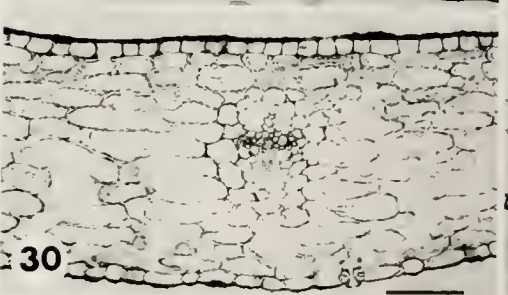
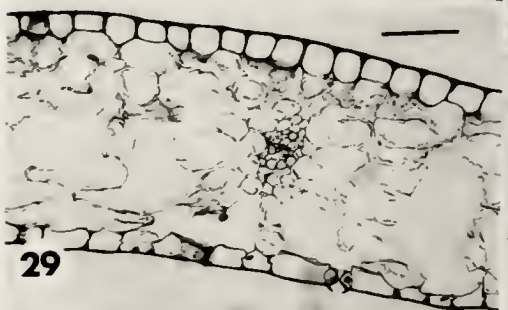
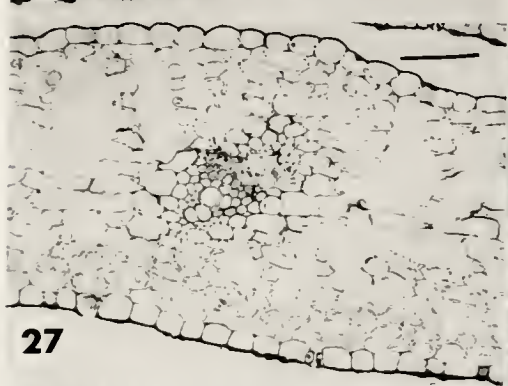
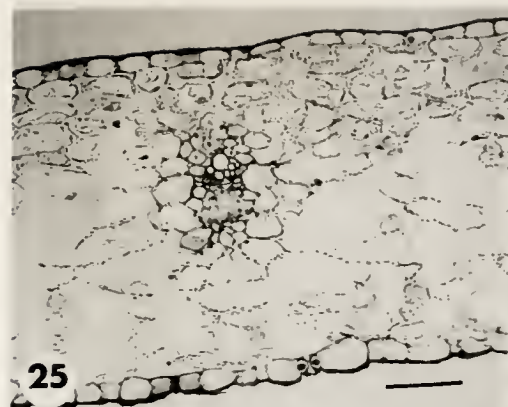


Figure 3.24. Leaf epidermal configurations of Eucharis and Caliphruria species and hybrid in the inter-costal area of the leaf. A. X Calicharis butcheri (Meerow 1110, FLAS). B. C. subdentata (Meerow 1123, FLAS). C. C. korsakoffii (Meerow 1096, FLAS).





Figures 3.25-3.31. Transverse sections of *Eucharis* and *Caliphruria* leaves. 25. *E. bonplandii* (Bauml 686, HUNT). 26. *E. astrophiala* (Madison 3792, SEL). 27-28. *E. formosa* (Meerow 1103, FLAS). 28. Tracheid with annular thickenings. 29. *E. bouchei* var. *dressleri* (Meerow 1107, FLAS). 30. *C. subdentata* (Meerow 1123, FLAS). 31. *C. korsakoffii* (Meerow 1096, FLAS). All scales = 100  $\mu$ m except 25  $\mu$ m in Fig. 28.



## CHAPTER IV FLORAL MORPHOLOGY

### Materials and Methods

#### Scanning Electron Microscopy (SEM)

Stigmas and seeds preserved in FAA were prepared and examined as described in Chapter III.

#### Anatomical Studies

Seeds preserved in FAA were prepared for parafin block sectioning as described for leaves in Chapter III. Scape sections were prepared freehand as described for petioles in Chapter III.

### Results and Discussion

#### Inflorescence

The inflorescence of Eucharis and Caliphruria is a naked scape typical of Amaryllidaceae. The scape is sub-terete in cross-sectional outline (Fig. 1), and has a solid pith. Vascular bundles are distributed in several concentric rings within the pith (Fig. 1). A layer of collenchyma cells occurs just below the epidermis of the scape.

The scape is terminated by two valvate-imbricate, ovate-lanceolate bracts that enclose several secondary bracts and the flower buds before anthesis. These bracts vary from green (E. subg. Heterocharis) to greenish-white (most species of subg. Eucharis) and are soon marcescent

after opening and spreading laterally. Each flower is subtended by a linear-lanceolate bracteole.

The inflorescence of the Amaryllidaceae is traditionally described as "umbellate". Developmental work by Mann (1959) on Allium, and Stout (1944) on Hippeastrum suggests that the superficially simple umbel of Amaryllidaceae actually represents a complex series of reduced, helicoid cymes. Anthesis occurs in a strict sequence within each cyme from the developmentally oldest flower to the youngest. The peripheral cymes flower first; the central cymes flower last.

Flower number varies in Eucharis and Caliphruria from 2-10, rarely as many as 12 (C. korsakoffii). Number of flowers is often a taxonomically useful character, though any species characterized by 8-10 flowers is capable of producing a depauperate inflorescence with fewer florets. An increase in flower number generally does not occur. In some species of subg. Eucharis (E. astrophiala, E. bouchei, E. ulei), a flower number of 5 has become virtually fixed. Reduction in flower number is usually considered the derived state in Amaryllidaceae (Traub 1962, 1963).

#### Flower Size and Fragrance

Flower size. The largest flowers in Eucharis are found in subg. Heterocharis, flowers of which average 7-8 cm in length. Flowers of Caliphruria are the smallest, never exceeding 4 cm in length. Subgenus Eucharis, the largest of the two subgenera of Eucharis, is variable, with flowers ranging from 3-7 cm in length. Within a fairly broad range, flower size can be used to distinguish phenetic species complexes within subg. Eucharis (see Chapters VI and XII), however, most species



of this subgenus are quite variable in size. Flower size may also be a factor of plant vigor and soil fertility. I have repeatedly noted differences from year to year in the size of flowers of greenhouse collections, depending on the relative health of the plant.

Floral fragrance. Subgenus Heterocharis is the only subgenus of Eucharis that is uniformly fragrant. The fragrance of all species of subg. Heterocharis is intense and sweet. Flowers of Caliphruria do not emit any detectable fragrance. Most species of E. subg. Eucharis are also without noticeable fragrance. In the few species of this subgenus that are fragrant (E. bakeriana, E. castelnaeana, E. formosa, and E. plicata subsp. brevidentata), the odor is not intense. In one case (E. formosa), the fragrance is slightly fetid. The significance of floral fragrance in Eucharis is discussed further in Chapter X.

### Perianth

The perianth of Eucharis and Caliphruria consists of six tepals in two whorls, basally connate into a tube of varying length and morphology. The tube of E. subg. Eucharis (Fig. 2E) is cylindrical for almost its entire length, abruptly dilating near the perianth throat. The tube of subg. Eucharis is also strongly curved, either abruptly just above the ovary (E. bakeriana, E. cyaneopserma), or gradually throughout the proximal half of its length (all other species). The curving of the tube results in the pendent habit of most species of subg. Eucharis. The tube is white for its entire length.

The tube of subg. Heterocharis (Fig. 2C, D) is tinted green proximally (for at least half its length). The tube is curved, though not as markedly as that of subg. Eucharis, and the habit of the flowers

is either declinate (E. anomala, E. sanderi) or sub-pendulous (E. amazonica). The tube is cylindrical for 1/2 to 2/3 of its length; it abruptly dilates in the distal half to 1/3. The tube morphology of X Calicharis butcheri (Fig. 2B), putatively an inter-subgeneric hybrid between E. sanderi and C. subedentata, is intermediate between Caliphruria (Fig. 2A) and E. subg. Heterocharis (Fig. 2C, D).

The tube of Caliphruria (Fig. 2A) is straight, and dilates gradually from base to throat. It is either sub-cylindrical (C. korsakoffii) or funnelform in shape (all other species). The tube is tinted green proximally (in C. subedentata, for 1/2 to 2/3 of its length).

The tepals of Eucharis and Caliphruria flowers are white. Those of the outer series are almost always longer and narrower than the inner tepals. The outer tepals are apiculate. The apiculum frequently has a small, papillate horn on the adaxial surface in E. subg. Eucharis. The inner tepals vary from acute to obtuse, sometimes minutely apiculate, at the apex.

The tepals of most species of subg. Eucharis spread at an angle of 90° or more from the throat. Perianth morphology of subg. Eucharis is thus predominantly crateriform. At times the tepals may be reflexed strongly above the midpoint of their length, or rarely for their entire length. Tepal habit varies even among flowers of the same inflorescence and shows no taxonomic consistency. If exposed to strong light, the abaxial midrib of the tepals of some species of subg. Eucharis may be lightly pigmented yellow.

The perianth of Caliphruria is infundibular. The tepals remain imbricate for half their length and spread distally at an angle of only



45-60°. The tepals of subg. Heterocharis are also, for the most part, imbricate proximally, and spread at 45-60° from the throat. The perianth is more or less campanulate in morphology. One species, E. amazonica, has the crateriform perianth characteristic of subg. Eucharis with a wide-spreading (ca. 90°) limb.

### Androecium

Staminal connation is one of the major characteristics of "infrafamily" Pancratioidinae. Some taxonomic workers have mistakenly considered the staminal cup of pancratioid genera homologous to the corona of Narcissus (e.g., Pax, 1888). The corona of Narcissus is of perianthal origin (Eichler, 1875; Arber, 1937), while the staminal cup of pancratioid taxa is composed entirely of androecial tissue (Arber, 1937; Singh, 1972).

The stamens of Eucharis and Caliphruria are variously connate proximally. In most species of subg. Eucharis and several species of subg. Heterocharis (E. anomala and E. amazonica), a conspicuous staminal cup or false corona is present (Fig. 3-4). In Caliphruria, the cup is reduced to a short, membranous, connate portion of the filaments near the perianth throat (Fig. 5). Eucharis sanderi (subg. Heterocharis) has a reduced staminal cup similar to that of Caliphruria.

Stamens of Eucharis and Caliphruria may be dentate, edentate or irregularly toothed. Both types of staminal morphology may occur in the same species, and variation may occur even among flowers of a single clone. The presence or absence of staminal dentation has frequently been overweighted in the alpha-taxonomic literature relating to these genera (e.g., Ravenna, 1982), but only occasionally has profound

taxonomic significance [e.g., E. astrophiala (Fig. 3), the only species of subg. Eucharis that always has an edentate staminal cup].

A variable pattern of green or yellow pigmentation is present in the androecium of all species of subg. Eucharis and Heterocharis. Stamens of Caliphruria are completely white. In subg. Heterocharis, the green (rarely yellowish) pigmentation is largely restricted to the interior of the cup, and extends into the dilated portion of the tube as well (Fig. 4). The coloration is concentrated along the filamental traces, but the tissue between the traces is suffused with green as well. In subg. Eucharis, pigmentation is present on both the exterior and interior surfaces of the cup, does not extend into the dilated portion of the tube, and takes the form of either broad spots below each free filament, or a uniform band of color at the basal 1/2 to 1/3 of the cup. In subg. Eucharis, the pattern is of limited taxonomic significance. Whether this pigmentation functions as nectar guides for pollinating animals is unknown.

The stamens of most species of subg. Eucharis constrict distally into a broadly subulate portion (> 1 mm wide for most of its length) of varying length. Only in two species, E. astrophiala (Fig. 3) and E. bouchei (in part), do the stamens constrict gradually from the rim of the staminal cup to the apex of the filament. The free filaments of Caliphruria are narrowly subulate (< 1 mm wide for most of their length, Fig. 5). The free filaments of E. sanderi (subg. Heterocharis) are narrowly subulate and slightly incurved. Those of E. anomala and E. amazonica are broadly subulate.

Anthers of Eucharis are introrse, dehiscing longitudinally and either dorsifixed or sub-basifixed in attachment. They are most

frequently oblong in shape, but are linear in subg. Heterocharis. At anthesis, the anthers of Caliphruria and E. subg. Eucharis are erect, but become versatile as they age. In subg. Heterocharis the anthers are versatile at anthesis.

### Gynoecium

Stigma and style. The flowers of almost all Eucharis and Caliphruria species are protandrous. Stigma receptivity does not occur until the second or third day following anthesis. In some cases, the stigma does not fully expand until the perianth has begun to senesce.

The styles of Eucharis and Caliphruria are usually exerted beyond the anthers, most frequently from 0.5-1 cm. In subg. Heterocharis, the styles are somewhat assurgent away from the stamens, and are exerted well over 1 cm past the anthers. In two species of subg. Eucharis, E. castelnaeana and E. plicata, the style is included within the cup. In the former species, autogamy seems to occur with regularity, and stigma receptivity coincides with anthesis.

The stigma of Eucharis and Caliphruria (Fig. 6, 8-9, 11-12) is obtusely trilobed. Trilobed stigmas are relatively rare in the Pancratioidinae, and Urceolina, sister group to Eucharis and Caliphruria, has a capitate, entire stigma. Traub and Moldenke (1949) and Traub (1963) considered a trilobed or trifid stigma the ancestral state in the Amaryllidaceae.

The stigmas of Eucharis and Caliphruria are papillate. The papillae of Eucharis are unicellular (Fig. 7, 13-16), while those of subg. Caliphruria (Fig. 10) are multicellular, consisting of both a stalk cell and globose head cell. X Calicharis butcheri, putatively a

natural hybrid of E. sanderi and C. subedentata has the multicellular stigmatic papillae (Fig. 17-18) characteristic of Caliphruria.

Heslop-Harrison and Shivanna (1977) characterized the stigmas of Eucharis and Caliphruria as dry-type, and suggested a correlation between this type of stigma morphology and sporophytic self-incompatibility. According to a number of workers (Heslop-Harrison, 1976; Kress, 1983; Larsen, 1977), however, gametophytic incompatibility is characteristic of monocots. At present, the incompatibility system of Eucharis and Caliphruria, though apparently present, is unknown (see Chapter X).

Ovary and ovules. The ovary of Eucharis and Caliphruria is inferior and contains septal nectaries. It is green, with the exception of two species, E. astrophiala and E. castelnaeana (subg. Eucharis) in which the ovary is white at anthesis. Ovaries of Eucharis and Caliphruria range from oblong-ellipsoid (subg. Heterocharis) to globose or sub-globose (subg. Eucharis and Caliphruria). The ovary of subg. Heterocharis is both trigonous and rostellate after senescence of the perianth. Ovaries of Caliphruria and subg. Eucharis are non-rostellate and smooth, with three exceptions: Eucharis bouchei var. bouchei, var. darienensis, and E. cyaneosperma have a trigonous ovary at anthesis.

The ovules of Eucharis and Caliphruria are globose, anatropous, and axile in placentation. Ovule number is quite variable throughout both genera. Within limits, however, ovule number is characteristic of species or species complexes. Subgenus Heterocharis has the largest ovule number in Eucharis, generally 16-20 per locule, but occasionally as low as 7 in E. sanderi (which otherwise has 16-20 throughout most of its range) and 9-12 in E. amazonica. In both subg. Eucharis and

Caliphruria, ovules do not number more than 10 per locule. Eucharis astrophiala, E. bouchei, E. bonplandii, E. cyaneopserma and E. ulei characteristically have 2 ovules per locule, but rarely as many as 5. In these species, there is a positive correlation between reduction in flower number and ovule number.

Traub and Moldenke (1949) and Traub (1962, 1963) considered numerous ovules an ancestral character in the Amaryllidaceae. In the Pancratioidinae, an ovule number of ca. 20 per locule characterizes the putatively ancestral complex of genera with typical, crateriform, pancratioid floral morphology, heavy floral fragrance and well-developed staminal cups (Meerow, 1985). Reduced ovule number is therefore likely a derived character state.

### Fruit and Seed

Fruit. The mature fruit of Eucharis and Caliphruria is a trilobulicidal capsule typical of the non-baccate fruited Amaryllidaceae. In fruit, the pedicel elongates to 2 or more times its length at anthesis. In Caliphruria and E. subg. Heterocharis (E. anomala), the capsule is thin-walled and green, sometimes turning yellow or brown at dehiscence. In subg. Eucharis, however, the capsule is leathery and bright orange (Fig. 19), contrasting vividly with the shiny black or blue seeds at dehiscence. It is probable, though unsubstantiated, that the combination of fruit and seed color functions mimetically to attract avian dispersal agents (sensu van der Pijl, 1982). This type of fruit morphology is unique among neotropical Amaryllidaceae. There is a single known exception to this characteristic fruit morphology in subg. Eucharis. Eucharis castelnaeana (Fig. 20) produces a capsule much like



that of Caliphruria. The fruit of this species is often tardily dehiscent, and sometimes abscises before opening, though the seeds within are ripe. The infructescence of E. castelnaeana bends to the ground (in all other species it remains erect), a habit noted in many Crinum species (Hannibal, 1972). In this manner, an indehiscent fruit might rot in contact with the substrate, thereby releasing the seeds.

Seed. Regardless of the number of ovules per locule in any species of Eucharis and Caliphruria, all but a few abort as the fruit matures. Generally 1-2 seeds are present per locule in mature capsules, but as many as four have been observed.

The seed of both Eucharis and Caliphruria is usually globose or ellipsoid and turgid, the consequence of copious endosperm and a high moisture content. Left at room temperature, the seeds will shrink away from the testa somewhat as moisture is lost, but are still capable of germination in this condition. Long-term viability has not been tested.

The seed of subg. Eucharis (Fig. 21) is characteristically ellipsoid, and has a shiny, smooth black (blue in E. cyaneosperma) testa. The single exception so far known is again E. castelnaeana (Fig. 22). The seed of this species is wedge-shaped by compression in the capsule, is less turgid than seeds of con-subgeneric species, and has a dull, rugose testa. The seed of E. anomala (subg. Heterocharis) is globose to very slightly compressed, and has a brown, slightly rugose testa.

In Caliphruria, the seeds of only C. korsakoffii and C. subedentata are known. Seeds of C. korsakoffii are globose, turgid, and have a smooth, lustrous brown testa. Seed of C. subedentata is slightly compressed, with a lustrous black, but rugose, testa.

Seed surface morphology (Fig. 23-28) does not reveal much taxonomically useful information. The testa is alveolate in all species examined. In E. bouchei var. dressleri (Fig. 24), abundant wax extrusions are found across the surface.

The testa of Eucharis and Caliphruria seeds is composed of phytomelan (Huber, 1969), a simple, largely inert, carbonaceous compound characteristically present in the seed coat of non-baccate fruited Amaryllidaceae (Huber, 1969; Dahlgren and Clifford, 1982). Werker and Fahn (1975) reported the occurrence of phenolic quinones in the phytomelan layer of Pancratium seeds. In most species of Eucharis and Caliphruria, the phytomelan layer is all that remains of the integuments (Fig. 30, 36). In E. bouchei, however, there is an additional layer of integument tissue, ca. five cells thick, interposed between the phytomelan and the endosperm (Fig. 34). Whether this may be a consequence of the tetraploid condition of this species is unknown. Most of the seed body of Eucharis and Caliphruria is taken up by a copious quantity of endosperm characterized by abundant transfer cells (Fig. 35). At maturity, no remnants of the nucellus were observed.

Most workers (e.g., Baker, 1888; Traub, 1963; Hutchinson, 1959; Dahlgren et al. 1985) have allied Eucharis and Caliphruria with Hymenocallis, Eurycles and Calostemma (i.e., tribe Eucharieae) on the basis of "fleshy seeds." The latter three genera do indeed have fleshy, bulbiform seeds that are sometimes viviparous, but they are not homologous structures.

The large, green seed of Hymenocallis is unique in a number of respects. The bulk of the seed body consists of two large, fleshy integuments with a well-developed vascular system and abundant



chlorenchymous tissue (Rendle, 1901; Whitehead and Brown, 1940). The embryo contains a large amount of stored starch (Whitehead and Brown, 1940). Whitehead and Brown (1940) characterized the seed, which does not undergo any period of dormancy, as intermediate between true vivipary and dormancy. Additionally, polyembryony has been observed frequently in seeds of Hymenocallis (Bauml, 1979; Rendle, 1901; Traub, 1966).

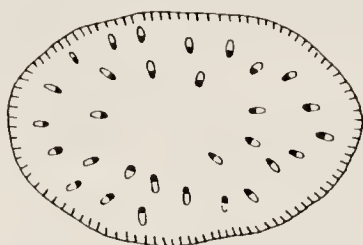
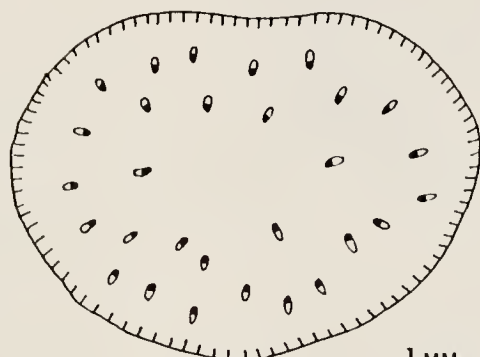
The seeds of Calostemma and Eurycles superficially resemble seeds of Hymenocallis, though they never achieve the size of the latter. According to a much-overlooked review of bulbiform seeds in Amaryllidaceae by Rendle (1901), the propagule of these two closely related Australasian genera is not actually a true seed, but represents an adventitious vegetative growth. After fertilization, at the chalazal end of a normal ovule, adventitious shoot and root growth occur and a true bulbil is formed. The integuments and the remnants of the nucellus form the bulbil's outer coat.

The turgid seed of Eucharis and Caliphruria, despite a high moisture content when first ripe, cannot be accurately described as fleshy. This becomes evident if the seed is allowed to dehydrate slightly at room temperature, and is most apparent in the hard seeds of E. castelnaeana, which, at capsule dehiscence, are less turgid than seeds of other species of subg. Eucharis. Seeds of Eucharis and Caliphruria have a reduced integument, represented in most cases only by the compressed phytomelan layer, and have never been observed to germinate viviparously. Phytomelan is absent from the testa of the pseudoseeds of Eurycles and Calostemma. It is present in only a single species of Hymenocallis, H. quitoensis Herbert (and possibly H.

heliantha Ravenna), which has been segregated into a separate genus, Lepidochiton Sealy (1937), on this basis.

Seeds of Pancratium are structurally most similar to those of Eucharis and Caliphruria. Though variable in morphology (Werker and Fahn, 1975), several species of Pancratium have a hard, turgid, compressed seed body with copious endosperm (Meerow, unpubl. data; Werker and Fahn, 1975). All species of Pancratium that I have examined have a phytomelanous testa with an alveolate testa. Seeds of Eucharis and Caliphruria do, however, have a higher moisture content than those of Pancratium, all species of which occur in xeric to seasonally dry habitats.

Figure 4.1. Serial tranverse sections through the scape of Eucharis  
castelnaeana (Schunke 14156, FLAS). p = proximal, m = medial, d =  
distal.

**d****m**

1 mm

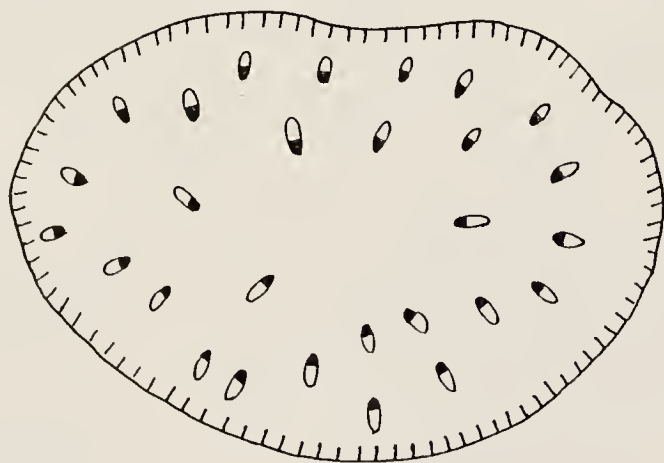
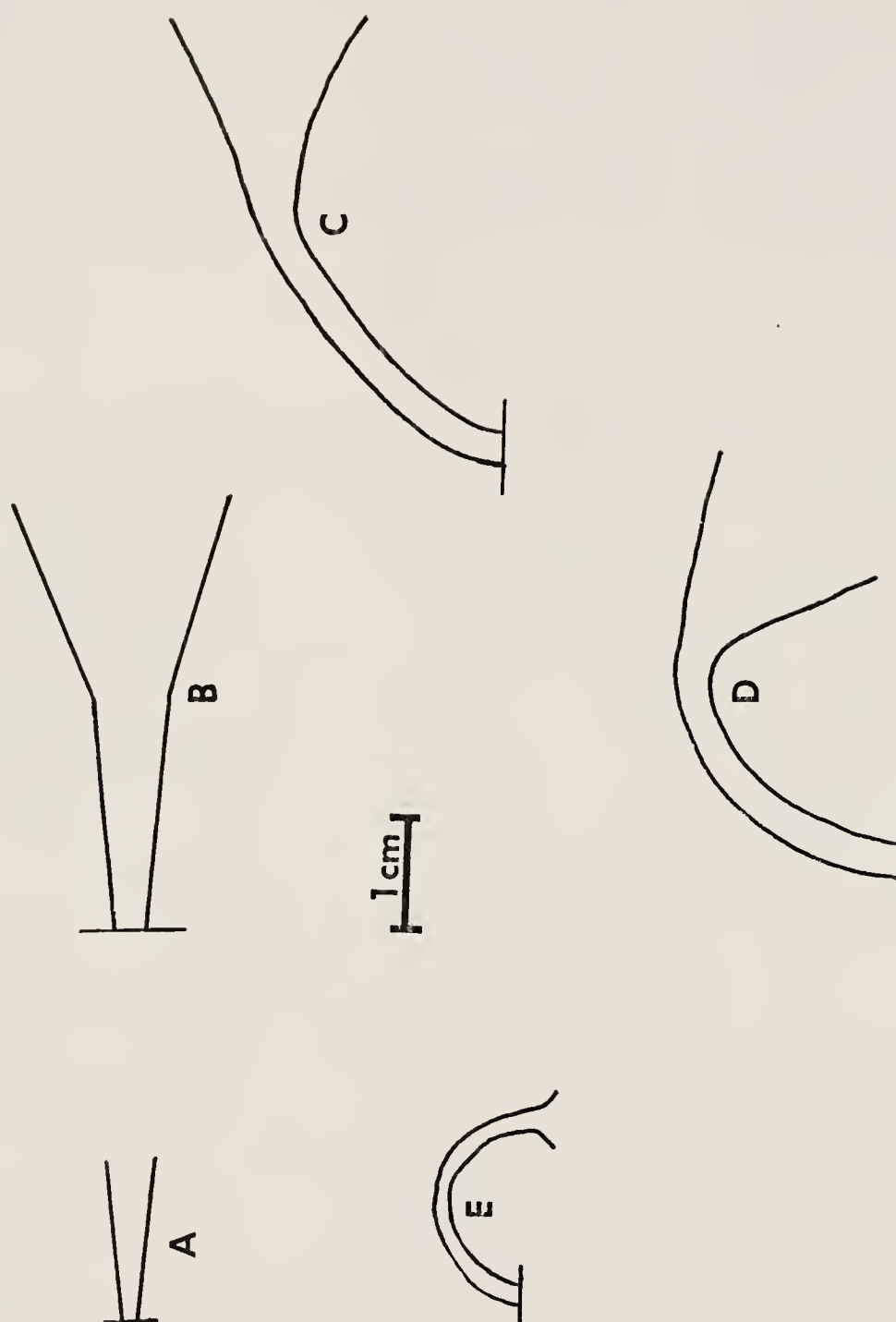
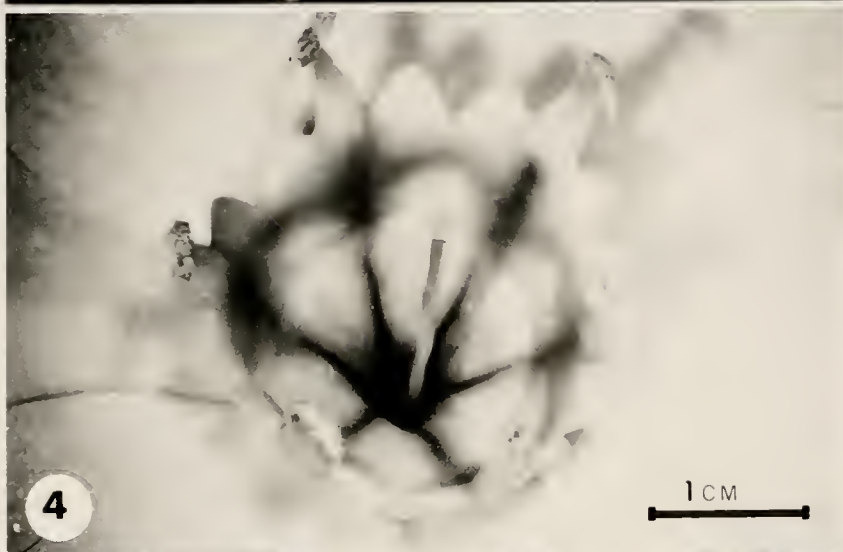
**p**

Figure 4.2. Perianth tube morphology of Eucharis and Caliphruria species or hybrids. A. C. subdentata (Meerow 1098, FLAS). B. X Calicharis butcheri (Meerow 1110, FLAS). C. E. sanderi (Cuatrecasas 16380, F). D. E. amazonica (Schunke 14179, FLAS). E. E. astrophiala (Madison 3792, SEL).

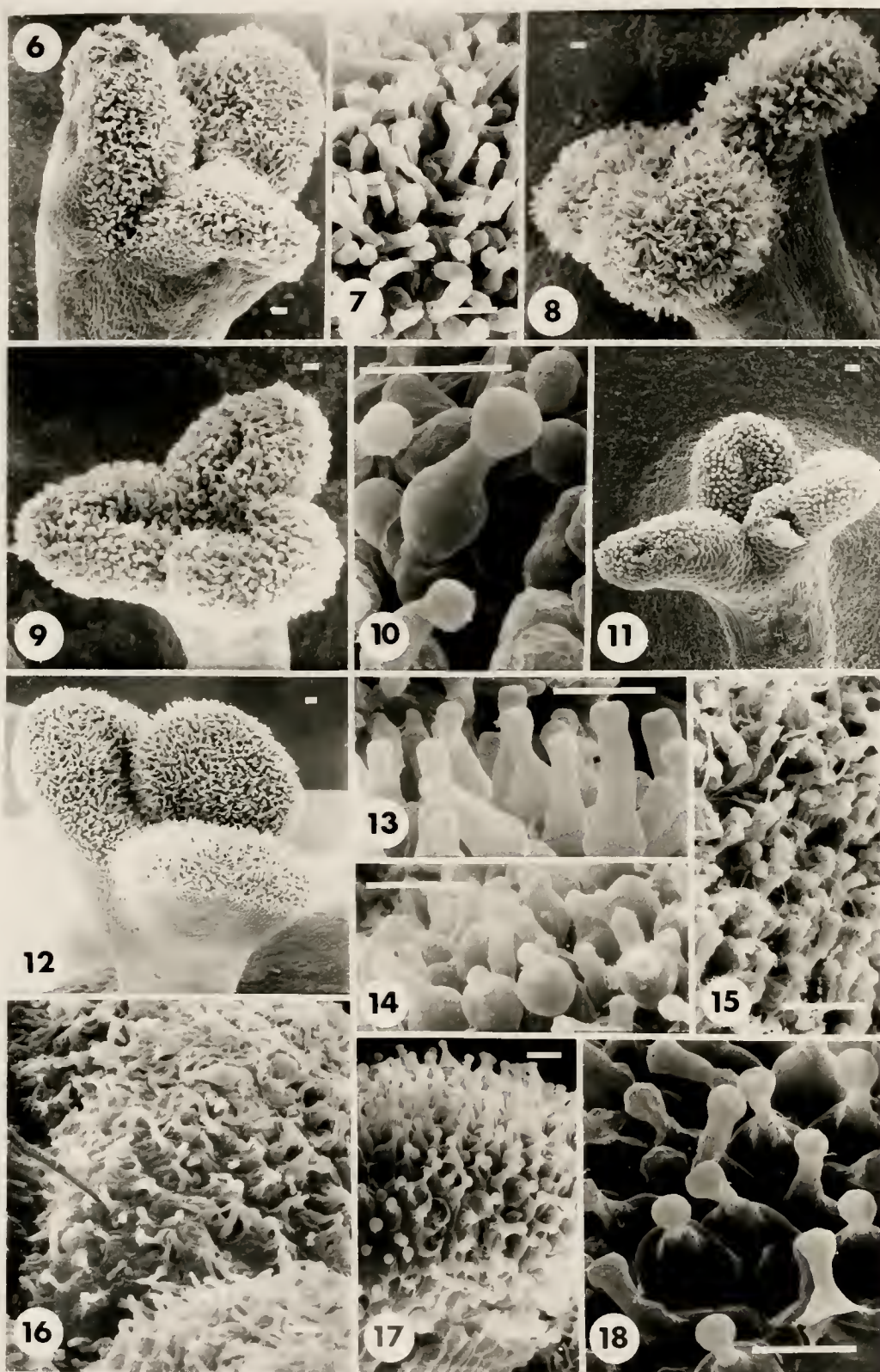




Figures 4.3-4.5. Androecial morphology of Eucharis and Caliphruria  
species. 3. E. astrophiala (Madison 3792, SEL). 4. E. amazonica  
(Schunke 14179, FLAS). 5. C. subedentata (Meerow 1109, FLAS).



Figures 4.6-4.18. SEM photomicrographs of Eucharis and Caliphruria  
stigmas. 6-7. E. astrophiala (Meerow 1111, FLAS). 8. E. plicata  
(Plowman 13941, FLAS). 9-10. C. subedentata (Meerow 1152). 11.  
C. korsakoffii (Meerow 1096, FLAS). 12-13. E. X grandiflora  
(Meerow 1127, FLAS). 14. E. anomala (Meerow 1141, FLAS). 15. E.  
sanderi (Cuatrecasas 16350, F). 16. E. amazonica (Schunke 14179,  
FLAS). 17-18. X Calicharis butcheri, Meerow 1110, FLAS). All  
scales = 50  $\mu$ m.



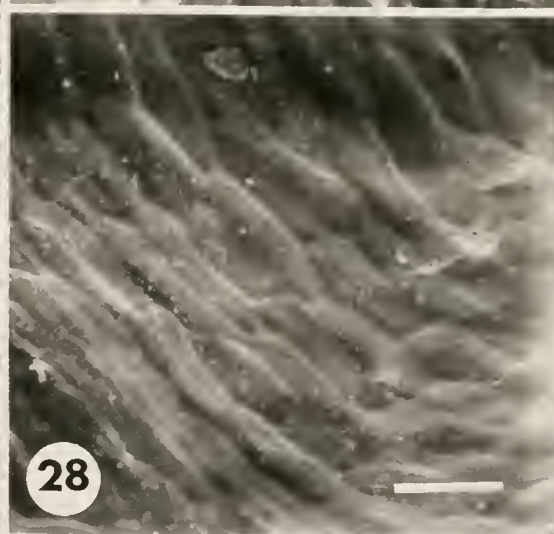
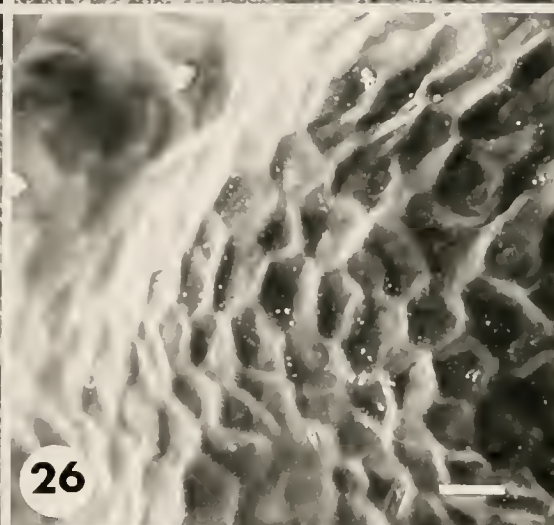
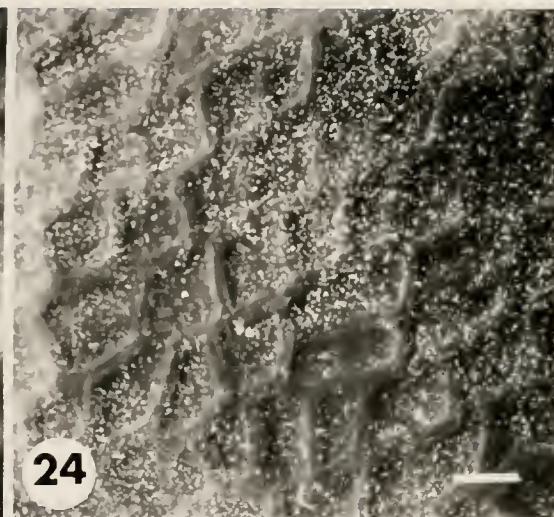
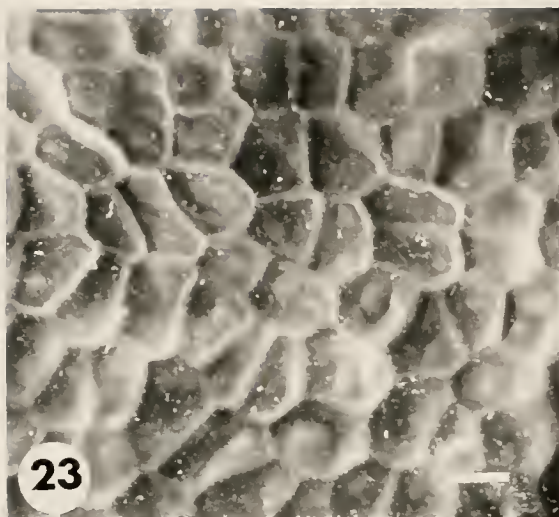
Figures 4.19-4.22. Fruits and seeds of Eucharis subg. Eucharis. 19-20.  
Mature capsules. 19. E. formosa (Schunke 14174, FLAS). 20. E.  
castelnaeana (Schunke 14156, FLAS). 21-22. Seeds. 21. E.  
bouchei var. bouchei (Meerow 1125, FLAS). 22. E. castelnaeana  
(Schunke 14156, FLAS).





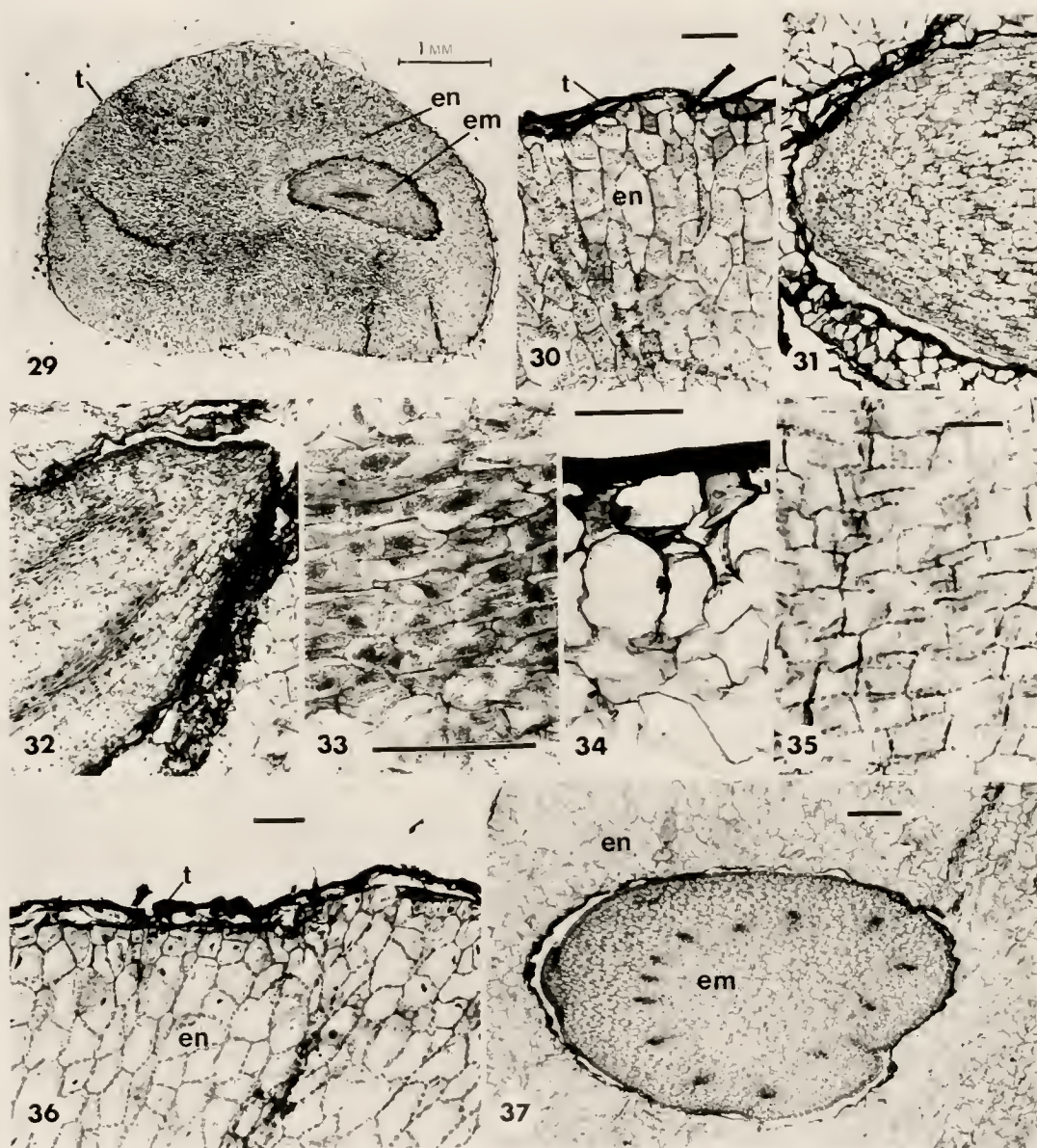


Figures 4.23-4.28. SEM photomicrographs of Eucharis and Caliphruria seed surfaces. 23. E. astrophiala (Meerow 1111, FLAS). 24. E. bouchei var. dressleri (Meerow 1107, FLAS). 25. E. formosa (Meerow 1103). 26. E. castelnaeana (Schunke 14156, FLAS). 27. C. korsakoffii (Meerow 1096, FLAS). 28. C. subdentata (Meerow 1152, FLAS).



Figures 4.29-4.37. Photomicrographs of Eucharis and Caliphruria seed anatomy. 29-33. C. korsakoffii (Meerow 1096, FLAS). 29. Longitudinal section through whole seed. 30. Transverse section through testa and part of endosperm. 31. Longitudinal section through radicle of embryo. 32. Longitudinal section through apex of embryo. 33. Longitudinal section through vascular initial of embryo. Scale = 40  $\mu$ m. 34-35. E. bouchei var. bouchei (Meerow 1125, FLAS). 34. Transverse section through testa. Note several layers of additional integument cells below outer phytomelan layer. 35. Endosperm. Note transfer tissue with pitted walls and plasmodesmata. 36-37. E. castelnaeana (Schunke 14156, FLAS). 36. Transverse section through testa and part of endosperm. 37. Transverse section through embryo. All scales = 100  $\mu$ m unless otherwise indicated. em = embryo, en = endosperm, t = testa.





## CHAPTER V POLLEN MORPHOLOGY

### Materials and Methods

#### Scanning Electron Microscopy (SEM)

Fresh, dehiscent anthers were removed from living collections, fixed in FAA, and pollen extracted. Pollen from herbarium specimens was treated according to the process of Lynch and Webster (1975). Samples were treated for and examined with SEM as described for leaf surfaces in Chapter III. Measurements of muri and lumina were derived from SEM photomicrographs.

#### Transmission Electron Microscopy (TEM)

Pollen grains were fixed for 12 hr in 3% glutaraldehyde in 0.1 M Na-cacodylate at pH 7.4, washed three times for 10 min with 7.5% solution of sucrose in 0.1 M Na-cacodylate at pH 7.4, post-fixed for 1 hr in 2%  $\text{OsO}_4$  in 0.1 M Na-cacodylate, washed as above three times for 10 min, and brought through an EtOH dehydration series. Dehydrated pollen was placed through two pure propylene oxide baths, then placed in 1:1 propylene oxide:epon for 1 hr, 1:2 propylene oxide:epon for 12 hr, and pure epon for 2-3 hr. Pollen was polymerized for 48 hr at 60° C, sectioned, and viewed on a Zeiss 10A electron microscope at 80 kv.

### Light Microscopy

Pollen size measurements were averaged for twenty grains examined with a Nikon Lapophot photomicroscope.

### Pollen Viability

Pollen was stained with Alexander's (1969) stain for 24 hrs at 50<sup>0</sup> C. Percentages given are based on the number of grains staining from a 200 grain sample.

### Statistical analysis

Correlations of pollen size with style length were performed with SAS release 5.08 on the Northeast Regional Data Center (NERDC) of the University of Florida.

### Terminology

Terminology follows Erdtman (1969) and Walker and Doyle (1975).

## Results

Pollen grains of all species of Eucharis and Caliphruria (Fig. 1-19) are boat-shaped elliptic, monosulcate, heteropolar, and bilateral in symmetry. The germination furrow (sulcus) runs the length of the presumed distal face of the grain (Fig. 12, 15). Exine sculpturing is semi-tectate-columellate and reticulate in all species examined (Fig. 1-19), composed of a network of muri (reticulum walls) and lumina (intervening gaps).



### Pollen Grain Size (Table 1)

Pollen grain size is quite variable in Eucharis and Caliphruria , and a notable size class (sensu Walker and Doyle, 1975) differential occurs between Eucharis and Caliphruria. Pollen of Eucharis falls into the large size class of Walker and Doyle (longest equatorial diameter 50-100  $\mu\text{m}$ ). Pollen of Eucharis has average longest equatorial diameters greater than 60  $\mu\text{m}$ , with two exceptions: E. castelnaeana and E. plicata subsp. brevidentata. Pollen of Caliphruria falls into the medium size class of Walker and Doyle (1975) with average longest equatorial diameters of near 50  $\mu\text{m}$ .

The greatest number of species of Eucharis have pollen grains with longest equatorial diameters between 65 and 75  $\mu\text{m}$ . Eucharis astrophiala (subg. Eucharis) has the largest pollen grains in the genus, with longest equatorial diameters of 83-86  $\mu\text{m}$ .

Polar diameter of pollen of Eucharis ranges from (39-) 45-60.6  $\mu\text{m}$ . Polar diameter less than 40  $\mu\text{m}$  is rare in these subgenera. Polar diameter of pollen of Caliphruria is always less than 40  $\mu\text{m}$ .

Considerable infraspecific variation pollen size is evident in some species of Eucharis (Table 1). Eucharis formosa is a wide-ranging and morphologically variable species (see Chapter XII). Longest average equatorial diameter among the populations sampled of this species shows a 12.7% difference between the smallest and largest value. The two subspecies of E. plicata show a 15% differential in pollen size. Other species are much more uniform in pollen grain size. Eucharis astrophiala is a narrow endemic restricted to western Ecuador with distinctive leaf and androecial morphology that is consistent among all populations. Three populations of this species sampled show only a 3.8%

difference. Eucharis bouchei, a tetraploid species also of limited distribution, but highly polymorphic, shows only a 2.4% difference between the largest and smallest values.

The smallest pollen grains in Eucharis and Caliphruria are found in species with the smallest flowers (Table 1), i.e., all species of Caliphruria and, in E. subg. Eucharis, E. castelnaeana. Nonetheless, one of the largest flowered species, E. sanderi (subg. Heterocharis) has small pollen grains relative to other large-flowered species. The largest pollen grains in the genus are found in E. astrophiala, a species at the smaller end of flower size range in the genus. Since style length is directly correlated with perianth size in Eucharis and Caliphruria, style length was tested for correlation with longest equatorial diameter of pollen of species in Table 1. Pearson correlation coefficient for style length with pollen size of 29 Eucharis and Caliphruria collections representing 16 species was only 0.379, and therefore not significant (significance is indicated by proximity of value to 1.000).

#### Exine Sculpturing (Fig. 1-19, Table 1)

The semi-tectate, reticulate exine sculpturing pattern of Eucharis and Caliphruria may be subdivided into three classes on the basis of lumina width. The first, designated Type 1 in Table 1, is characteristic of most species of Eucharis (Fig. 1-11, 13, 15-16).. The reticulum of Type 1 exine is coarse, with largest lumina widths equal to or greater than 5  $\mu$ m. Type 1 exine can be further subdivided on the basis of muri width. In Type 1-A (Fig. 3-11, 13, 15-16), the muri are equal to or greater than 1  $\mu$ m wide. This is the most common exine morphology of

Eucharis. In Type 1-B exine, the muri are less than 1  $\mu\text{m}$  wide. This is characteristic of a single species of subg. Eucharis: E. astrophiala (muri ca. 0.6  $\mu\text{m}$  wide, Fig. 1-2).

In Type 2 exine, lumina are 2-3  $\mu\text{m}$  wide, and a marked reduction in reticulum coarseness occurs at the meridional faces of the grain. Only two species of Eucharis have Type 2 morphology, E. oxyandra (subg. Eucharis, Fig. 12), E. sanderi (subg. Heterocharis, Fig. 14), and one species of Caliphruria, C. korsakoffi (Fig. 19). Width of the muri, however, is variable among the species with Type 2 sculpturing, ranging from less than 0.4  $\mu\text{m}$  in E. oxyandra, to ca. 0.75  $\mu\text{m}$  wide in E. sanderi, and ca. 1  $\mu\text{m}$  wide in C. korsakoffi.

Type 3 exine sculpturing is only characteristic of the Colombian species of Caliphruria (Fig. 17-18). Type 3 sculpturing is finely reticulate with lumina only 1-2  $\mu\text{m}$  wide, and the muri 0.5-0.6  $\mu\text{m}$  wide. As in Type 1 sculpturing, the reticulum is predominantly consistent in coarseness throughout the grain surface.

#### Pollen Wall Ultrastructure (Fig. 20-31)

Eucharis and Caliphruria pollen grains are remarkably uniform in their exine stratification patterns. They are completely ectexinous in composition. The columellae arise from a thin foot-layer (usually ca. 2  $\mu\text{m}$  thick), and the intine is as thick or thicker than the exine. The tectum is quite fragile, and usually ca. 5  $\mu\text{m}$  thick. No channelling is apparent in either the exine or intine.

### Discussion

Large, boat-shaped-elliptic, monosulcate pollen grains with reticulate exine morphology are the most common type of pollen found in the Amaryllidaceae (Erdtman, 1952; Meerow and Dehgan, 1985; Walker and Doyle, 1975). Similar morphology has been reported for many Liliaceae sensu lato (Erdtman, 1952; Walker and Doyle, 1975; Zavada, 1983), and conforms to the fossil form genus Liliacidites Couper, one of the major angiosperm pollen types described from early Cretaceous deposits (Doyle, 1973; Walker and Walker, 1984). This type of pollen morphology appears to be basic to the monocotyledonous orders in general (Doyle, 1973). Among the Amaryllidaceae, only one group of genera show a radical departure from this basic pollen morphology. Crinum and its allies [tribes Crineae (Pax) Traub and Strumarieae Salisb. sensu Traub (1963)], all have bisulcate pollen and spinulose exine sculpturing (Dahlgren and Clifford, 1982; Erdtman, 1952; Nordal et al., 1977; Meerow, unpubl. data). With the exception of Crinum, these genera are restricted to Africa, many of them endemic to South Africa. In a remarkable example of convergence, Donoghue (1985) reported a similar divergence in Caprifoliaceae.

The Type 1 exine morphology that is characteristic of most Eucharis pollen seems to have phylogenetic significance within "infrafamily" Pancratioidinae (Meerow, 1985; Meerow and Dehgan, 1985). All or some of the species of each of the genera with putatively primitive pancratioid floral morphology (i.e. Eucharis, Hymenocallis, Pamianthe Stapf, Pancratium, and Paramongaia Velarde) have large to very large, coarsely reticulate pollen. The pollen of related genera with

divergent floral morphology shows reduction trends in both size and reticulum coarseness (Meerow, 1985; Meerow and Dehgan, 1985).

Reduction in size and reticulum coarseness have been considered evolutionary trends for angiosperm pollen in general (Walker and Doyle, 1975). Colombian species of Caliphruria (Fig. 17-18) show the greatest degree of divergence for these pollen characters in comparison with Eucharis.

The differentiation of the reticulum into coarse and fine areas, characteristic of species with Type 2 exine, is restricted to monocot pollen (Doyle, 1973; Walker and Walker, 1984), and has been observed in some Liliacidites pollen from the early Cretaceous (Walker and Walker, 1984). The evolutionary polarity of this character is unclear, however. Meerow and Dehgan (1985) described a transformation series from auriculate pollen through dimorphic reticulum to homogeneous reticulum among the subgenera of Hymenocallis (sensu Traub, 1962, 1980), which would suggest that the homogeneous reticulum is an advanced character state. The three species with dimorphic exine sculpturing (E. oxyandra, Fig. 12; E. sanderi, Fig. 14; and C. korsakoffi, Fig. 19) each represent isolated taxa of their respective genus or subgenera (see Chapter XI). The dimorphic reticulum in these three species may thus be symplesiomorphous. On the other hand, each of three species differ in muri width, thus the Type 2 exine morphology may have had an independent, and thus derived, origin in each of the three.

In width of both muri and lumina, the pollen of E. oxyandra (Fig. 12) resembles that of Urceolina, sister group to Eucharis, though pollen of the latter genus fits the medium size class of Walker and Doyle, and does not exhibit a substantial differentiation of the reticulum into



coarse and fine areas (Fig. 1 in Chapter XI). Eucharis oxyandra is a problematic species morphologically as well, with certain characters of intermediacy between Eucharis and Urceolina, particularly in androecial morphology (see Chapter XII). I have suggested that E. oxyandra may represent a relict taxon related to the ancestor of Urceolina, or a possible intergeneric hybrid (see Chapter XII), but this species is at present too poorly known to confirm any of several hypotheses concerning its origins.

Zavada (1984) associates reticulate exine sculpturing with sporophytic self-incompatibility (SSI). Though the SI system of Eucharis and Caliphruria, if present, is unknown, two morphological characters of the genus-- pollen sculpturing, and stigma type (Heslop-Harrison and Shivanna, 1979)-- have been correlated with sporophytic SI, despite the fact that only gametophytic SI has been reported for monocots (Heslop-Harrison, 1976; Kress, 1981; Larsen, 1977).

Kress and Stone (1982) reviewed pollen wall ultrastructure of monocots. The lack of endexine in the pollen grain wall appears to be a virtually universal characteristic of monocot pollen. The thin foot-layer and columellate structure of the exine found in Eucharis and Caliphruria is common to all other genera of the Pancratioidinae that I have examined (Meerow, unpubl. data; Meerow and Dehgan, 1985), and may be basic to the Liliflorae in general (Doyle, 1973; Walker and Walker, 1984). The pattern of exine stratification in the pancratioid Amaryllidaceae thus appears highly conserved.

Pollen grain size and style length has been correlated in some investigations (Baker and Baker, 1979; Lee, 1978; Plitmann and Levin, 1983; Schnack and Covas, 1945; Taylor and Levin, 1975) but not in others



(Cruden and Miller-Ward, 1981; Darwin, 1896; Germeraad et al., 1968; Ganders, 1979; Hammer, 1978). Cruden and Lyon (1985) observed that all studies which showed a strong correlation involved related species, while non-correlating studies involved unrelated taxa. They tested correlations between both style length and stigma depth (an approximation of the distance a pollen tube must grow to reach exogenous resources in the transmission tissue of the style) and pollen grain volume among species of several genera in several families. Cruden and Lyon concluded that style length has little correlation with pollen size, while stigma depth was highly correlated with style length. Where style length and pollen grain volume do correlate, i.e., among related species, they suggest that phylogeny, rather than function, is represented. They further conclude that pollen grains need not contain sufficient endogenous resources to reach the ovules, but only enough for pollen tubes to grow through the stigma and reach exogenous substances in the styler transmission tissue.

In Eucharis and Caliphruria as a whole, little correlation between style length and pollen grain size (as represented by longest equatorial diameter, rather than volume) is evident (Table 1). Stigma depth, in so far as I understand Cruden and Lyon's determination of this measure, does not seem to vary appreciably among species of Eucharis. The stigma of E. astrophiala, the species with the largest pollen grains in Eucharis, is no larger or "deeper" than that of E. plicata, the species of subg. Eucharis with the smallest pollen grain.

### Conclusions

In characteristics of pollen grain size (medium size class), and exine sculpturing (Type 3), Caliphruria shows the greatest degree of divergence from the putatively ancestral, large, coarsely reticulate pollen grain characteristic of most species of Eucharis. The Type 1 exine sculpturing of Eucharis shows relationship to the pollen morphology of other genera of infrafamily Pancratioidinae with similar floral morphology, i.e., Hymenocallis, Pamianthe, Pancratium and Paramongaia (Meerow, 1985; Meerow and Dehgan, 1985).

Pollen grain size in Eucharis does not demonstrate any obvious correlation with flower size (= style length). The large amount of variation in pollen grain size in a few species of Eucharis may suggest that this character, under certain conditions, is subject to as much infraspecific variation as characters of vegetative and floral morphology.

Table 5.1. Pollen morphology and style length of Eucharis and Caliphruria species. All voucher specimens are deposited at FLAS unless otherwise stated.

TAXON	VOUCHER	POLAR DIAMETER ( $\mu\text{m}$ )	LONGEST EQUATORIAL DIAMETER ( $\mu\text{m}$ )	EXINE <sup>a</sup> TYPE	STYLE LENGTH (mm)
<u>Eucharis</u> subg. <u>Eucharis</u>					
<u>E. astrophiala</u>	Meerow 1152	60.64 (+ 4.83)	84.43 (+ 4.72)	1-B	37.0
	Madison 3792 (SEL)	58.62 (+ 4.16)	86.19 (+ 4.90)		46.8
	Dodson et al. 7182 (SEL)	60.55 (+ 2.87)	83.05 (+ 4.71)		50.0
<u>E. bakeriana</u>	Meerow 1108	50.70 (+ 2.24)	76.85 (+ 3.32)	1-A	52.0
<u>E. bonplandii</u>	Bauml 686 (HUNT)	43.50 (+ 3.01)	62.95 (+ 2.73)	1-A	44.5
<u>E. bouchei</u> var. <u>bouchei</u>	Meerow 1125	48.93 (+ 4.70)	68.43 (+ 4.22)	1-A	38.0
	Meerow 1157	45.70 (+ 4.30)	66.80 (+ 3.14)		50.0
<u>E. bouchei</u> var. <u>dresleri</u>	Meerow 1107	49.65 (+ 1.11)	68.30 (+ 2.10)	1-A	59.5

Table 5.1--continued.

TAXON	VOUCHER	POLAR DIAMETER ( $\mu\text{m}$ )	LONGEST EQUATORIAL DIAMETER ( $\mu\text{m}$ )	EXINE <sup>a</sup> TYPE	STYLE LENGTH (mm)
<u>E. candida</u>	Meerow 1144	49.75 (+ 1.09)	69.50 (+ 2.69)	1-A	37.0
	Meerow 1158	46.75 (+ 3.06)	68.70 (+ 1.82)		49.3
	Dodson et al. 14095 (SEL)	52.30 (+ 3.35)	72.15 (+ 3.17)		-
	Schunke 14155-B	50.00 (+ 2.39)	73.00 (+ 2.51)		40.0
<u>E. castelnaeana</u>	Schunke 14156	39.45 (+ 1.28)	55.80 (+ 2.73)	1-A	23.5
<u>E. cyaneosperma</u>	Meerow 1032	47.95 (+ 2.38)	67.55 (+ 2.06)	1-A	50.0
<u>E. formosa</u>	Meerow 1099	47.70 (+ 2.45)	65.50 (+ 3.07)		60.5
	Meerow 1103	47.70 (+ 2.95)	69.00 (+ 3.00)	1-A	51.0
	Meerow 1159	51.11 (+ 1.89)	73.84 (+ 2.58)		56.8

Table 5.1--continued.

TAXON	VOUCHER	POLAR DIAMETER ( $\mu$ m)	LONGEST EQUATORIAL DIAMETER ( $\mu$ m)	EXINE <sup>a</sup> TYPE	STYLE LENGTH (mm)
	<u>Besse et al. s. n.</u> <u>(SEL)</u>	48.50 (+ 3.04)	70.65 (+ 3.15)		59.8
	<u>Schunke 14157</u>	47.75 (+ 2.19)	72.50 (+ 2.80)		52.8
	<u>Schunke 14171</u>	52.00 (+ 2.15)	71.50 (+ 2.66)		49.6
<u>E. oxyandra</u>	<u>Hutchison et al.</u> <u>5983 (UC)</u>	42.36 (+ 3.48)	68.36 (+ 3.53)	2	32.8
<u>E. plicata</u> subsp. <u>plicata</u>	<u>Plowman 13951</u>	43.45 (+ 3.50)	68.90 (+ 1.84)	1-A	27.5
<u>E. plicata</u> subsp. <u>brevidentata</u>	<u>Meerow 1143</u>	41.30 (+ 3.10)	59.90 (+ 3.01)	1-A	32.0
<u>E. ulei</u>	<u>Meerow 1024</u>	49.35 (+ 2.61)	69.85 (+ 3.04)	1-A	44.6

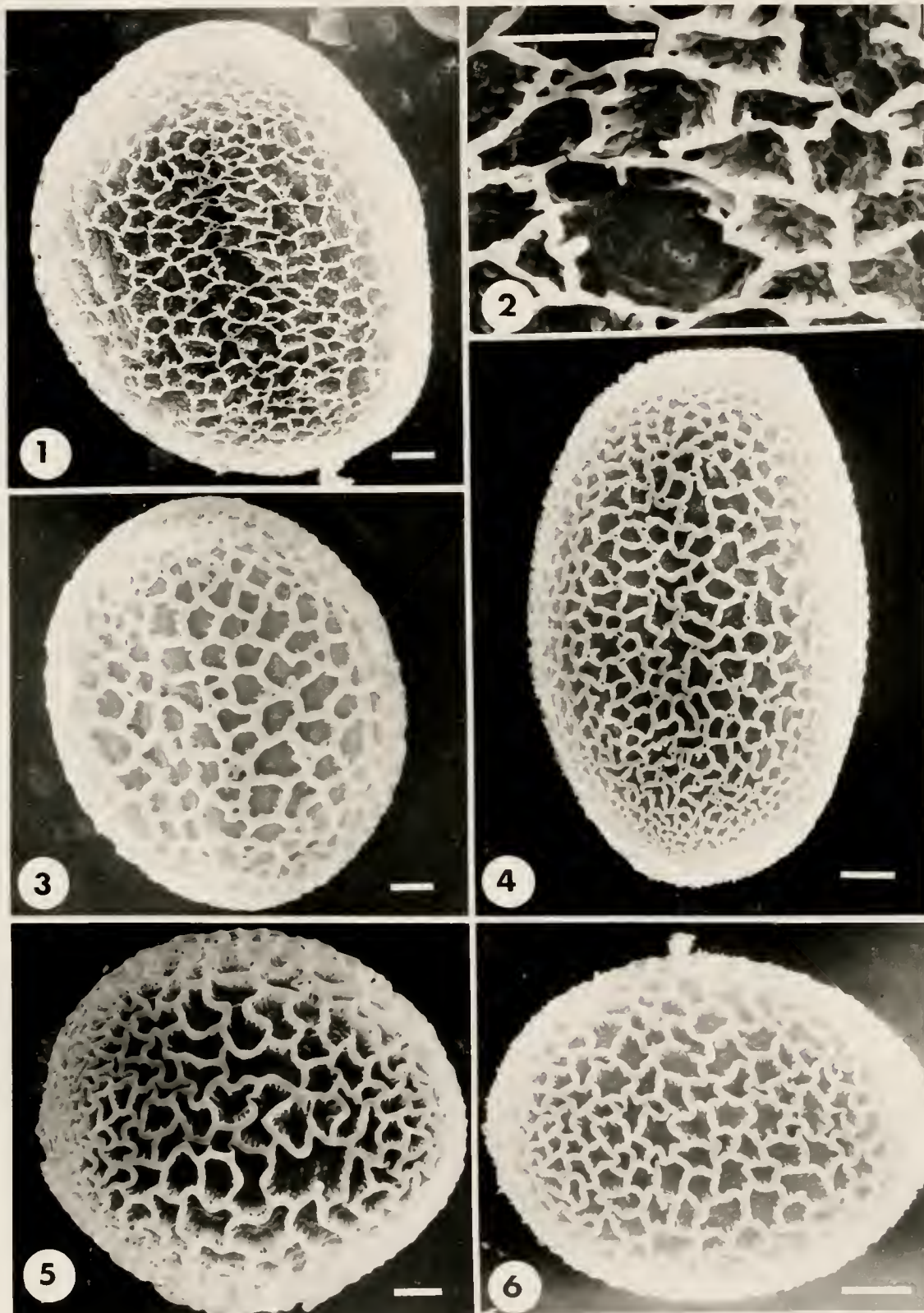
Table 5.1--continued.

TAXON	VOUCHER	POLAR DIAMETER ( $\mu\text{m}$ )	LONGEST EQUATORIAL DIAMETER ( $\mu\text{m}$ )	EXINE <sup>a</sup> TYPE	STYLE LENGTH (mm)
<u>Eucharis subg. Heterocharis</u>					
<u>E. amazonica</u>	Schunke 14179	51.65 (+ 2.67)	78.25 (+ 3.39)	1-A	71.4
<u>E. anomala</u>	Meerow 1141	48.55 (+ 2.89)	71.15 (+ 3.69)	1-A	58.5
<u>E. sanderi</u>	Cuatrecasas 16380 (F)	39.75 (+ 3.01)	61.15 (+ 2.13)	2	76.0
<u>Caliphruria</u>					
<u>C. korsakoffi</u>	Meerow 1096	32.30 (+ 2.47)	50.35 (+ 2.94)	2	16.0
<u>C. subdentata</u>	Meerow 1152	39.25 (+ 3.63)	50.95 (+ 3.28)	3	31.0
<u>C. tenera</u>	Triana 1289 (COL)	35.20 <sup>b</sup>	53.70 <sup>b</sup>	3	-

<sup>a</sup>See text for explanation.<sup>b</sup>Values without standard deviations were derived from statistically insignificant quantities of pollen.

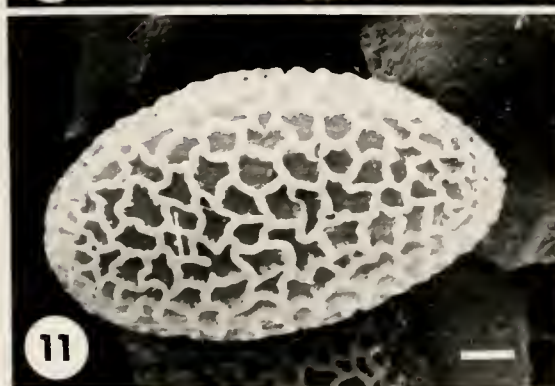
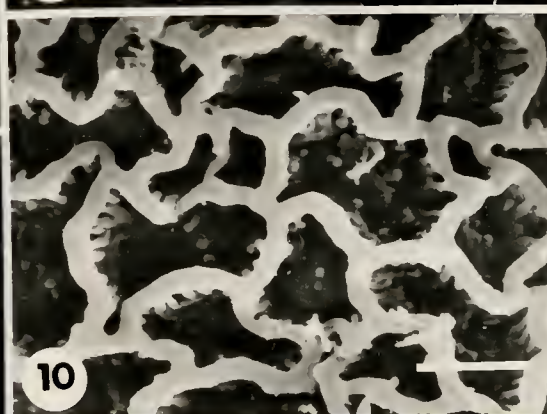
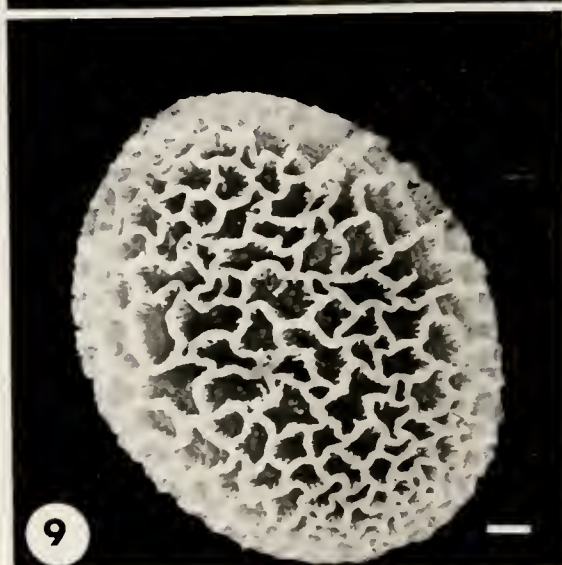
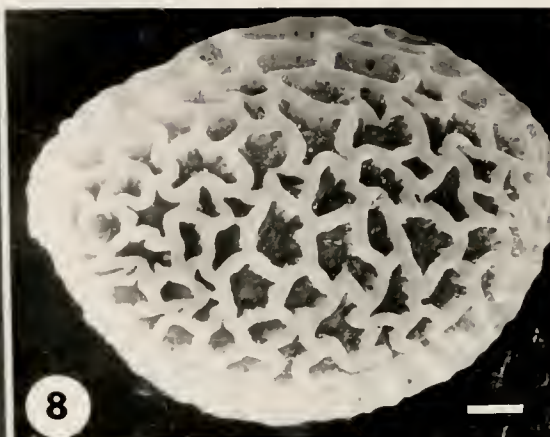


Figures 5.1-5.6. SEM photomicrographs of *Eucharis* pollen grains. 1-2. *E. astrophiala* (Madison 3792, SEL). 1. Whole grain, proximal polar view. 2. Exine sculpturing. 3-6. Whole grains, proximal polar views. 3. *E. bonplandii* (Bauml 686, HUNT). 4. *E. bouchei* var. *dressleri* (Meerow 1107, FLAS). 5. *E. candida* (Asplund 19120, S). 6. *E. castelnaeana* (Schunke 14156, FLAS). All scales = ca. 5  $\mu$ m.



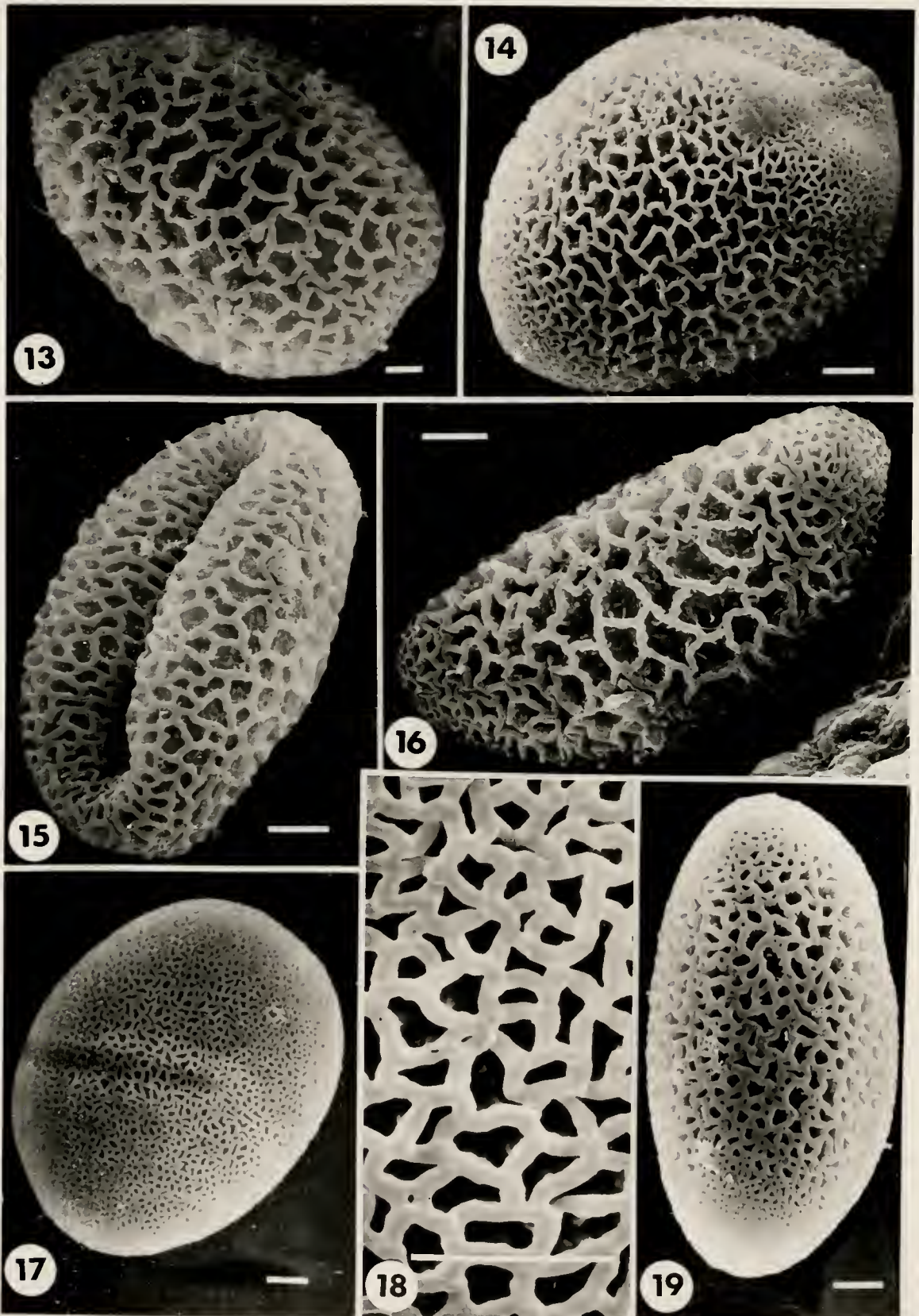
Figures 5.7-5.12. SEM photomicrographs of *Eucharis* pollen grains. 7-8.  
Whole grains, proximal polar view. 7. *E. corynandra* (Ravenna  
2090, K). 8. *E. cyaneosperma* (Seibert 2145, US). 9-10. *E.*  
*formosa* (Meerow 1103, FLAS). 9. Whole grain, proximal polar view.  
10. Exine sculpturing. 11-12. Whole grains, proximal polar view.  
11. *E. plicata* (Meerow 1025, FLAS). 12. *E. oxyandra* (Hutchison et  
al. 5983, UC), oblique distal polar view. All scales = ca 5  $\mu$ m.





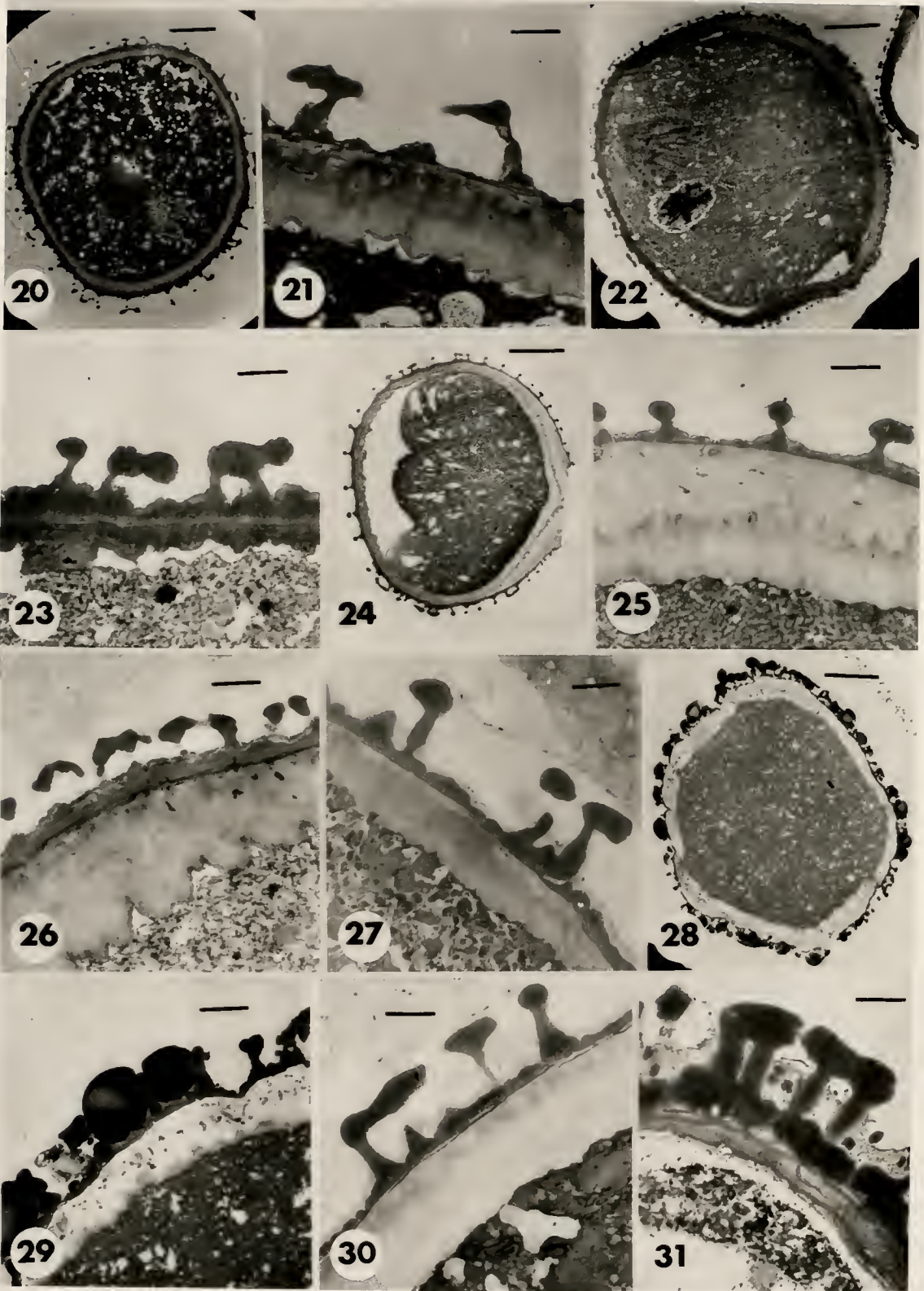
Figures 5.13-5.19. SEM photomicrographs of Eucharis and Caliphruria pollen grains. 13-17. Whole grains. 13. E. amazonica (Asplund 13214, S), proximal polar view. 14. E. sanderi (Killip 35401, US), oblique lateral longitudinal view. 15. X Calicharis butcheri (Meerow 1110, FLAS), oblique distal polar view. 16. E. X grandiflora (Meerow 1127, FLAS), lateral longitudinal view. 17-18. C. subdentata (ex hort s. n., K). 17. Distal polar view. 18. Exine sculpturing. 19. C. korsakoffi (Meerow 1096, FLAS). All scales = ca 5  $\mu$ m.







Figures 5.20-5.31. TEM photomicrographs of Eucharis and Caliphruria pollen grain sections. 20, 22, 24, and 28. Whole grain sections. Scale = 10  $\mu$ m. 21, 23, 25-27, 29-31. Sections through pollen grain wall. Scale = 1  $\mu$ m. 20-21. E. astrophiala (Meerow 1111, FLAS). 22-23. E. bouchei var. bouchei (Meerow 1157, FLAS). 24-25. E. plicata var. plicata (Meerow 1025). 26. C. subdentata (Meerow 1152, FLAS). 27. E. anomala (Meerow 1141, FLAS). 28-29. E. sanderi (Cuatrecasas 16380, F). Black globules are extruded lipids. 30. E. amazonica (Meerow 1105, FLAS). 31. E. X grandiflora (Meerow 1127, FLAS).



## CHAPTER VI PHENETIC ANALYSES

The genus Eucharis presents a bewildering mosaic of morphological variation which severely limits the accuracy of alpha-taxonomic species delimitations. For example, characters such as flower size and androecial dentation have been utilized to distinguish species without any reference to how such characters might vary within populations and throughout a species' range.

Principle Component analysis (PCA) is a widely employed ordination methodology assessed as complementary to hierarchical cluster analysis (Crisci et al, 1979; Sneath and Sokal, 1973). Both PCA and cluster analysis allow quantitative analysis of continuous variation across numerous morphological characters among a number of operational taxonomic units (OTU's). The PCA algorithm rotates the axes representing the characters to positions that will concentrate maximum variance in the least number of axes. The axes are called principle components. Scattergrams may be generated from principle components, and heuristic relationships of the OTU's thus visualized. Clifford and Stephenson (1975) warn against the utilization of PCA as a classification device, particularly when insufficient cumulative variation is represented in the first few principle components. PCA and associated clustering algorithms provide a means to 1) quantify such patterns of variation, and 2) graphically represent relationships based

on overall similarity in a manner that may aid in the final assessments of taxonomic relationships.

### Materials and Methods

Principle component and hierarchical cluster analyses of selected herbarium specimens were conducted with CLUSTAN 2 vers. 2.1, originated by the computing laboratory of the University of St. Andrews, Scotland, on the North Florida Regional Data Center (NERDC) system of the University of Florida. Three dimensional scattergrams were constructed from PCA factor scores utilizing a program written by Bart Schutzman (University of Florida).

Raw data was standardized using the "z-score" method (Sneath & Sokal, 1973), by which initial values for each character were replaced by standard deviations from the mean value for that character. A distance matrix was then calculated using squared euclidean distance (Cormack, 1971).

Twenty-seven characters were initially used in the analyses. Examination of the results suggested that some of these characters (e.g., all foliage characters, scape height, ovary length) were unreliable due to environmental plasticity, developmental variation, or specimen preparation. Though living material provides additional characters of potential utility (e.g. leaf surface texture, pigmentation pattern of the staminal cup), the inability to consistently determine these characters in dried specimens precluded their inclusion. Where any two characters were highly correlated (more than 80% correlation), which can result in data redundancy (Sneath and Sokal, 1973), one of the



two characters was removed from the data matrix, except where I felt their removal would result in loss of information. In the final analyses, 17 floral characters (Table 1) were selected as the basic data set, of which fourteen were continuous, quantitative characters. The remaining three qualitative characters were treated by assigning a numerical value for each state of the character. Since CLUSTAN would treat these values as continuous, every attempt was made to number the character states in a progressive transformation series, such that any two successive numbers would reflect putative character state relationship. These transformation series were constructed by careful study of morphological patterns and trends in the genus Eucharis, and comparative study with closely related genera of Amaryllidaceae.

At the level of species delimitation, analysis needs to begin with individuals (Sneath and Sokal, 1973). A representative sampling of populations is desirable (Williams and Lance, 1965), but in a widely-dispersed genus such as Eucharis with many rare and inaccessible species, in which a single genet in nature may function effectively at the level of a population, or where an entire species is represented by a single collection, a logical starting point is the use of all available individuals.

Problems of taxonomic delimitation in Eucharis are concentrated in Amazonian populations of subg. Eucharis. An additional area of difficulty is the highly polymorphic, tetraploid E. bouchei complex of Central America. Analyses of these two groups utilized 78 and 20 OTU's respectively. The inclusion in these analyses of well-marked species, or species groups, whose delimitations are resolved by more traditional systematic methodologies was deemed superfluous. The inclusion of such

OTU's can distort the analysis by introducing large additional variance over some of the characters (Sneath and Sokal, 1973).

In addition to the larger analysis of all Amazonian populations (including in this group a few OTU's from central Colombia), I subjected one subset of this large matrix to additional analyses. This smaller group represents populations of E. candida and E. formosa from eastern Ecuador, a monophyletic species complex that appeared taxonomically insoluble from examination of herbarium specimens alone. These populations are not only well-collected, but the specimens are of high quality.

Staminal dentation in Eucharis has historically been an important criterion from which species lines have been drawn. Analyses of the Amazonian populations and the Napo-Pastaza populations were repeated with characters of androecial dentation removed from the matrix. As overall androecial morphology has been used frequently to delimit species of Eucharis, a final analysis of 82 OTU's representing Amazonian populations was conducted, using only the eight androecial characters of the original character set (characters 3-5, 12-16). OTU lists and data matrices for all analyses can be found in Appendix I.

A number of sequential, agglomerative, hierarchical, non-overlapping (SAHN) clustering methods (Sneath and Sokal, 1973) have been devised for analyzing phenetic data, e.g., Lance and Williams' (1967) complete linkage, Sokal and Michener's (1958) average linkage [unweighted pair group method of analysis (UPGMA) of Sneath and Sokal, 1973], and Ward's (1963) minimum variance method. While the same distance matrix is used by all three methods, each differs from the others by its procedure for determining clusters between distances.



Complete linkage increases the distance between existing clusters, making it difficult for OTU's to join, thus tending to create new clusters (Cormack, 1971; Sneath and Sokal, 1973; Clifford and Stephenson, 1975). Average linkage does not affect the ability of individuals to join extant clusters. Ward's method uses least intra-group and greatest inter-group variance in determining where to fuse clusters. Average linkage (UPGMA) was chosen for the cluster analyses of Eucharis on the basis of preliminary analyses of various data sets using all three methods described. Little difference was apparent among the dendrograms generated by the three algorithms. In each case, however, average linkage seemed to provide the most parsimonious clustering of species groups.

## Results

### Amazonian Eucharis Populations (Table 2-4, Figs. 1-6)

PCA (Figs. 1-3). Cumulative variance of 67.2% in 17 characters across 78 OTU's (Table 2) was resolved within the first three principle components (PC's). Characters 2 (limb spread), 5 (stamen width), 7 (tube width at throat), and 9 (inner tepal length) contributed the most variance to PC1, the component with the highest percentage variance (45.5%). Characters 1 (flower number), 9, 13 (staminal cup width), and 15 (cleft of staminal cup) contributed most of the variance to PC2, especially character 15. Characters 5, 6 (tube length), 9, and 14 (toothing) were most strongly represented in PC3.

Removal of characters 14 and 16 (androecial toothing) raised the cumulative variance within the first three PC's by only 1.5% to 68.7%.

Removal of these two characters slightly changed the character components of the PC's (Table 3). Character 6 (tube length) replaced 7 in PC1, and characters 8 (outer tepal length) and 12 (cup length) were more important contributors than 9 and 15 in PC2. Character 12 also replaced the deleted character 14 in relative contribution to PC3.

The scattergrams generated by these PC scores (Figs. 1-2) are not appreciably different. In both, two main phenetic groups can be distinguished (E. formosa and E. castelnaena/plicata), but neither with absolute clarity. An even more amorphous group comprises the remaining four species. Eucharis formosa and E. castelnaeana (and plicata) represent the extremes of flower size (largest and smallest respectively) among the OTU's. The E. formosa aggregation segregates into two smaller groups in Fig. 1 on the basis of staminal dentation. When this character is removed from the analysis, E. formosa becomes a more homogeneous phenetic group. Among OTU's representing E. candida, removal of characters 14 and 16 had less impact. The single outlying OTU representing the rare E. bakeriana moves closer to the E. formosa group when characters of staminal dentation are removed from the data set (Fig. 2).

Phenetic resolution of E. bonplandii, E. candida, E. cynaeosperma and E. ulei is poor in both Figs. 1 and 2. These species overlap to a large extent in flower size. Eucharis candida, in particular, shows extreme heterogeneity.

Ordination with only the eight androecial characters (3-5, 12-16) resolved 72.7% of total variance in PC's 1-3 (Table 3). Characters 3 (length of free filament), 5 (width of stamen), and 13 (cup width) contributed the greatest amount of variance to PC1; 3, 12 (cup length)

and 14 (toothing) to PC2; and 3, 14, and 16 (relative length of tooth) to PC3. Though the E. castelnaeana/plicata and E. formosa groups show a tendency to segregate, there is a greater degree of breakdown between these two large phenetic groups. The poorly resolved assemblage of OTU's representing E. bonplandii, candida, E. cyaneosperma and E. ulei are well-dispersed among the two larger phenetic groups. Eucharis bakeriana is isolated from all other OTU's.

Cluster analyses (Figs. 4-6). Dendrograms generated by hierarchical cluster analysis largely confirm the results of PCA. Using the complete data set (Fig. 4), the average linkage algorithm resolved three large clusters. All OTU's representing E. castelnaeana cluster at a distance coefficient (DC) of 1.073. OTU's representing E. plicata subsp. plicata join this cluster at a DC of 1.736. Almost all OTU's representing E. formosa cluster at a DC of 1.423. This large cluster includes the solitary OTU representing E. bakeriana, one putative hybrid between E. candida and E. formosa, and two OTU's representing E. candida. One of the latter (OTU 74), however, is an outlying addition to one of the smaller component clusters. All other species did not fare as well. Paralleling the results of PCA, most OTU's representing E. bonplandii, E. candida, E. cyaneosperma and E. ulei, form a large, heterogeneous cluster at a DC of 1.858, within which may occur smaller clusters of 2-4 conspecific OTU's. This heterogeneous group joins the E. formosa cluster at DC 1.984.

Removal of staminal toothing characters (Fig. 5) did not alter the innermost topology of the dendrogram appreciably. However, the E. castelnaeana group, rather than forming a distinct cluster independent

of the other clusters, is joined to the heterogeneous species cluster at DC 1.825.

The dendrogram based on analysis of only staminal characters (Fig. 6) is largely in concordance with that produced by the larger data set, with E. formosa dominating one main cluster, and all other species another. The two OTU's representing E. plicata subsp. plicata, however, do not join with E. castelnaeana until the latter has clustered with the heterogeneous OTU's (DC 1.974). Most edentate OTU's of E. formosa form a distinct subgroup within the first large cluster.

#### Eastern Ecuadorean Eucharis (Table 5-6, Figs. 7-10)

PCA. Cumulative variance of 64.8% in 17 characters was resolved within the first three PC's across 28 OTU's. Character 6 (tube length) contributed the most variance to PC1, followed by 2 (limb spread), 12 (cup length), and 15 (cleft of the staminal cup). Characters 1 (flower number), 10 (width of inner tepal), 13 (cup width) and 14 (toothing) are mostly expressed in PC2. Characters 3 (length of free filament), 9 (inner tepal length), 10 and 15 are the most important contributor's to PC3.

Removal of characters 14 and 16 (staminal dentation) raised the cumulative variance only 0.5% (Table 6). Major contributors to the variance of each PC were characters 2, 5, 7, and 8 (PC1); 1, 12 and 13 (PC2); and 2, 4, 6 and 8 (PC3).

The scattergrams generated by these PC scores (Figs. 7-8) are similar. Eucharis formosa and E. candida form distinct phenetic groups, largely on the basis of flower size, with two putative hybrids falling between the two species groups. Staminal dentation separates two

subgroups in both species (Fig. 7), a distinction that disappears if these characters are eliminated from the data matrix (Fig. 8). In both scattergrams, a single outlying OTU (no. 27 in Table 5, Appendix 1) is found among the E. candida group along PC2. This specimen has sharply acute staminal teeth, rare in E. candida, and very short inner tepals (9.4 mm).

Cluster analyses (Figs. 9-10). Hierarchical cluster analysis largely conforms to the results of PCA for this group. In the dendrogram produced with all 17 characters, two main clusters are formed, E. formosa at DC 2.062, and E. candida at DC 1.767. However, both species groups cluster soon after, at DC 2.519. A single outlying OTU occurs in each species group, OTU 3 (E. formosa), and 27 (E. candida). Within each species group, further clustering on the basis of presence or absence of staminal teeth is evident. The E. candida outlying OTU does not fuse with the other OTU's until after both species groups have formed a single cluster (DC 4.375). One of the putative hybrids clusters with the E. formosa OTU's, the other with E. candida. The dendrogram for the reduced data matrix is much the same in topology, with an expected decrease in the amount of clustering of toothed or edentate forms of each species.

#### Eucharis bouchei complex (Table 7, Figs. 11-13)

PCA (Figs. 11-12). Cumulative variance of 71.9% percent across 20 OTU's was resolved in the first three PC's. Characters 5 (stamen width), 6 (tube length), 9 (inner tepal length) and 14 (toothing) contributed the greatest magnitude of variance to PC1, especially character 6. PC2 is largely a measure of outer tepal length (character



8), inner tepal width (11), staminal cup width (13) and tothing (14). Characters 1, 7, and 14 also substantially contributed to the variance reflected in PC2. Characters 2 (limb spread), 3 (length of free filament), 13 (staminal cup width), and 15 (tothing) were the most important sources of variance in PC3.

The three varieties of E. bouchei do not clearly resolve into three phenetic groups in Fig. 11. Though var. bouchei shows a tendency to assemble along PC2 (21.1% total variance), this variety is still widely distributed along PC1 (38.7% total variance). One OTU each of var. darienensis (no. 11) and dressleri (no. 2) form an outlying group, as do OTU's 6, 7, and 15 of var. bouchei. Variety darienensis shows a measure of phenetic congruence, but intergradation between it and variety bouchei is still evident.

If the scattergram for the E. bouchei complex is reformatted so that PC2 and PC3 are visually accentuated (Fig. 12), grouping of OTU's becomes largely a measure of androecial variance. In this scattergram, the three varieties are resolved more clearly, particularly var. bouchei. Variety darienensis, however, still intergrades with several OTU's of var. bouchei. One of these OTU's (8), however, was collected from Cerro Campana in Panama Province, an area of sympatry between these two varieties. The third (no. 7) is a Costa Rican collection.

Cluster analysis (Fig. 13). Two major clusters are resolved in the UPMGA dendrogram, each fairly heterogeneous. The first clusters at a DC of 1.356. An outlying OTU (one of two representing var. darienensis) fuses with this cluster at DC 1.921. Within this first cluster, two subgroups emerge at DC's 1.207 and 1.213 respectively. The former is made up entirely of OTU's representing var. darienensis. The

second is represents var. bouchei, with the single exception of OTU 5 (var. darienensis). OTU 5 forms together with OTU 8 (var. bouchei) an outlying cluster to this second subgroup.

The second major cluster is formed at a DC of 2.502, near where all clusters finally merge (DC 2.779). This smaller cluster is more heterogenous than the first, but four OTU's of var. bouchei cluster at a DC of 2.112. As in PCA, OTU's 2 and 11 (var. dressleri and darienensis respectively) form a phenetic group.

### Discussion

Most species of Eucharis, particularly those with the widest distributions, exhibit a high level of morphological diversity. Most species found in the Amazon basin, for example, overlap to some degree in quantitative floral characters (see Chapter XII). Such characters are often the only ones available from herbarium material, unless the collectors techniques and field notes have been meticulous. The results of these phenetic studies not only confirm this variability, but also resolve some morphological patterns in the genus.

The presence or absence of staminal dentation, among Amazonian species of the genus, is a character of little or no taxonomic value. This is evident in the PCA scattergrams (Figs. 1-2, 5-6) of Amazonian and eastern Ecuadorean populations. Removal of these characters from the analysis causes the immediate intergradation of any phenetic groups based largely on this character. The use of eight androecial characters by themselves did not successfully resolve phenetic groups among 87 OTU's from Amazonian populations.

In terms of resolving phenetic groups on the basis of 17 floral characters, PCA and UPMGA were least successful with the large set of 78 OTU's representing Amazonian populations. Only E. castelnaeana, the smallest-flowered species of Eucharis subg. Eucharis, and most OTU's of E. formosa, the largest, were resolved phenetically as distinct groups. Species of intermediate flower size (E. bonplandii, E. candida, E. cyaneosperma, and E. ulei), form a large, heterogenous mosaic. Sneath and Sokal (1973) warn of this problem when large, heteromorphic OTU sets are chosen for analysis.

Phenetic analysis was more successful with smaller groups of OTU's representing only 2 species or a single, polymorphic species complex. The results of phenetic analyses of these two smaller groups can also be compared with results of electrophoretic analysis of the same groups for any correlative patterns.

Populations of E. candida and E. formosa in the Oriente of Ecuador segregate as distinct phenetic groups. The resulting scattergrams (Figs. 7-8) and dendrograms (Figs. 9-10) also suggest that hybridization has occurred between these sympatric species. Patterns of genetic variation (Chapter VIII) suggest a possible monophyletic origin of both species in the Pastaza valley of Ecuador, with subsequent radiation into adjoining areas. Radiation and secondary contact may have occurred more than once. Infra-cluster variation does not show any geographic congruence among the two species groups.

The Central American E. bouchei semi-species complex does not resolve phenetically as cleanly as the candida/formosa group. Staminal cup morphology, however, does separate varieties to a fair degree (Fig. 12). Floral size characters in this group (Fig. 11) do not succeed as

well in resolving phenetic groups. Thus, the situation is exactly opposite that of the eastern Ecuadorean species. The taxa of the E. bouchei group are tetraploid, putatively allotetraploid, and have even higher levels of heterozygosity than the diploid Ecuadorean taxa (Chapter VIII). Geographic isolation has probably been an important factor restricting gene flow between populations (and consequently some varieties) of E. bouchei. By contrast, populations of E. candida and E. formosa in eastern Ecuador are often sympatric.

### Conclusions

Patterns of morphological variation in Eucharis are best resolved by phenetic analyses when the OTU population represents only a few closely related taxa. The degree of phenotypic plasticity in continuous characters of floral size results in poor clustering of taxonomic groups on the basis of such data, particularly when the OTU population is highly heteromorphic. The presence or absence of staminal dentation is not a taxonomically significant character among Amazonian species of Eucharis.

Analysis of the eastern Ecuadorean populations of E. candida and E. formosa supports their treatment as distinct species, and suggests that hybridization has occurred between them. Varieties of E. bouchei resolve into relatively distinct phenetic groups only when androecial characters are emphasized.

Species of Eucharis are usually rare, widely dispersed in their natural habitats, and characteristically form small populations. If most species are pollinated by female euglossine bees flying long

distances between populations, the potential for gene flow, maintenance of heterozygosity, and consequent morphological diversity, is large. The poor resolution of phenetic groups, particularly among species of intermediate floral size, is probably a reflection of these factors.

In a recent review of morphological variation and speciation, Davis and Gilmartin (1985) cite developmental factors (e.g., canalization, plasticity, epistasis) which weaken the correlation of genetic and morphological divergence. They further conclude that morphological divergence can proceed in random direction among plants. The tendency to recognize taxonomic species in Eucharis, based on narrow concepts of morphological discontinuity, is at variance with much of the phenetic patterns that occur within the genus, and is further weakened by what is known about the genetics, chromosome cytology, and reproductive biology of the group. Morphological divergence in Eucharis may be mostly a factor of rapid chromosomal change (see Chapter VII) and peripheral isolation (Chapter IX). Where these evolutionary forces are less acute, as among the taxa of the Amazon basin, phenetic groups are much more difficult to distinguish.



Table 6.1. Characters used for multivariate analysis of Eucharis species.

1. Flower number.	6: edentate
2. Limb spread (mm).	15. Cleft of staminal cup
3. Length of free filament (mm).	0: none
4. Width of free filament (mm).	1: < 1/5 length of cup
5. Width of stamen (mm).	2: 1/5-1/3 length of cup
6. Length of tube (mm).	3: 1/3-1/2 length of cup
7. Width of tube at throat (mm).	4: > 1/2 length of cup
8. Length of outer tepal (mm).	16. Relative length of teeth:
9. Length of inner tepal (mm).	0: edentate.
10. Width of outer tepal (mm).	1: < 1/2 length of filament.
11. Width of inner tepal (mm).	2: 1/2 length of filament.
12. Staminal cup length (mm).	3: = length of filament.
13. Staminal cup width (mm).	4: > length of filament.
14. Toothing of staminal cup:	17. No. ovules per locule.
1: bidentate, teeth acute	
2: bidentate, teeth obtuse	
3: irregularly toothed	
4: quadrate	
5: lobed	

Table 6.2. First three principle components for multivariate analysis of Amazonian Eucharis.

CHARACTER NUMBER	COMPONENT NUMBER		
	1	2	3
1	0.073	0.331	0.232
2	0.461	0.029	-0.153
3	0.242	-0.048	-0.115
4	-0.113	0.019	0.282
5	-0.400	0.033-	0.469
6	-0.276	0.086	-0.308
7	0.404	-0.039	0.238
8	0.181	-0.145	-0.094
9	0.353	0.288	-0.431
10	-0.162	0.053	0.162
11	-0.170	0.028	-0.174
12	-0.209	-0.059	0.304
13	-0.185	-0.160	-0.102
14	0.105	0.148	-0.286
15	0.106	-0.847	-0.139
16	-0.005	-0.006	0.048
17	0.009	-0.019	-0.037
PERCENT OF VARIANCE	45.47	12.76	9.94

Table 6.3. First three principle components for multivariate analysis of Amazonian Eucharis (characters of staminal dentation removed).

CHARACTER NUMBER	COMPONENT NUMBER		
	1	2	3
1	0.090	0.337	0.231
2	0.553	-0.029	-0.225
3	0.246	0.019	-0.201
4	-0.013	-0.034	-0.209
5	-0.365	0.054	-0.538
6	0.484	-0.083	0.342
7	0.191	-0.134	-0.079
8	-0.342	-0.305	0.314
9	-0.198	-0.014	0.269
10	-0.152	0.114	-0.193
11	-0.142	-0.024	0.012
12	0.147	-0.145	-0.432
13	0.006	-0.853	-0.022
15	0.010	-0.033	0.046
17	0.009	-0.021	-0.039
PERCENT OF VARIANCE	49.57	11.17	7.94

Table 6.4. First three principle components for multivariate analysis of Amazonian Eucharis (androecial characters only).

CHARACTER NUMBER	COMPONENT NUMBER		
	1	2	3
3	0.360	0.418	0.423
4	-0.087	-0.115	-0.275
5	-0.528	0.292	0.256
12	-0.212	-0.453	-0.156
13	-0.626	-0.055	0.290
14	0.089	0.521	-0.371
15	0.182	-0.308	-0.286
16	0.325	-0.391	0.593
PERCENT OF VARIANCE	42.98	19.49	10.26

Table 6.5. First three principle components for multivariate analysis of eastern Ecuadorean Eucharis.

CHARACTER NUMBER	COMPONENT NUMBER		
	1	2	3
1	0.119	0.374	0.182
2	0.310	0.076	0.033
3	-0.199	0.041	-0.458
4	0.093	0.096	-0.275
5	0.201	0.037	0.168
6	0.723	-0.062	0.115
7	-0.020	-0.063	-0.325
8	0.043	-0.122	-0.121
9	-0.054	0.142	0.396
10	0.213	0.192	-0.411
11	-0.006	0.082	-0.215
12	0.307	0.093	-0.025
13	0.215	-0.585	0.037
14	-0.062	-0.620	0.015
15	0.284	0.014	-0.347
16	-0.049	0.139	0.148
17	0.025	0.034	-0.054
PERCENT OF VARIANCE	36.33	16.51	11.92



Table 6.6. First three principle components for multivariate analysis of eastern Ecuadorean Eucharis (characters of staminal dentation removed).

CHARACTER NUMBER	COMPONENT NUMBER		
	1	2	3
1	0.137	0.381	0.175
2	0.355	0.010	0.342
3	0.058	0.046	-0.075
4	-0.076	-0.119	0.387
5	-0.633	0.035	-0.274
6	0.146	-0.061	-0.393
7	-0.418	-0.055	0.164
8	-0.338	0.110	0.459
9	-0.150	-0.191	-0.094
10	-0.181	0.158	-0.304
11	-0.196	-0.041	0.136
12	0.087	-0.774	0.054
13	0.035	0.370	0.118
15	0.183	0.133	-0.304
17	-0.010	0.038	-0.028
PERCENT OF VARIANCE	40.40	14.98	9.85

Table 6.7. First three principle components for multivariate analysis of the Eucharis bouchei complex.

CHARACTER NUMBER	COMPONENT NUMBER		
	1	2	3
1	0.151	0.317	0.120
2	-0.265	-0.189	0.340
3	-0.244	0.112	-0.440
4	-0.197	-0.141	-0.147
5	-0.375	0.129	0.059
6	-0.615	0.099	0.133
7	0.032	-0.302	-0.116
8	-0.100	-0.336	-0.106
9	-0.404	0.069	-0.061
10	0.017	0.168	-0.239
11	-0.030	0.386	0.137
12	0.156	-0.062	-0.045
13	0.013	-0.353	-0.524
14	-0.232	-0.381	0.216
15	-0.184	0.322	-0.436
16	-0.007	0.056	-0.121
17	-0.046	-0.195	0.020
PERCENT OF VARIANCE	38.71	21.12	12.03

Figure 6.1. PCA scattergram based on variance across 17 floral characters in 78 OTU's representing Amazonian Eucharis.

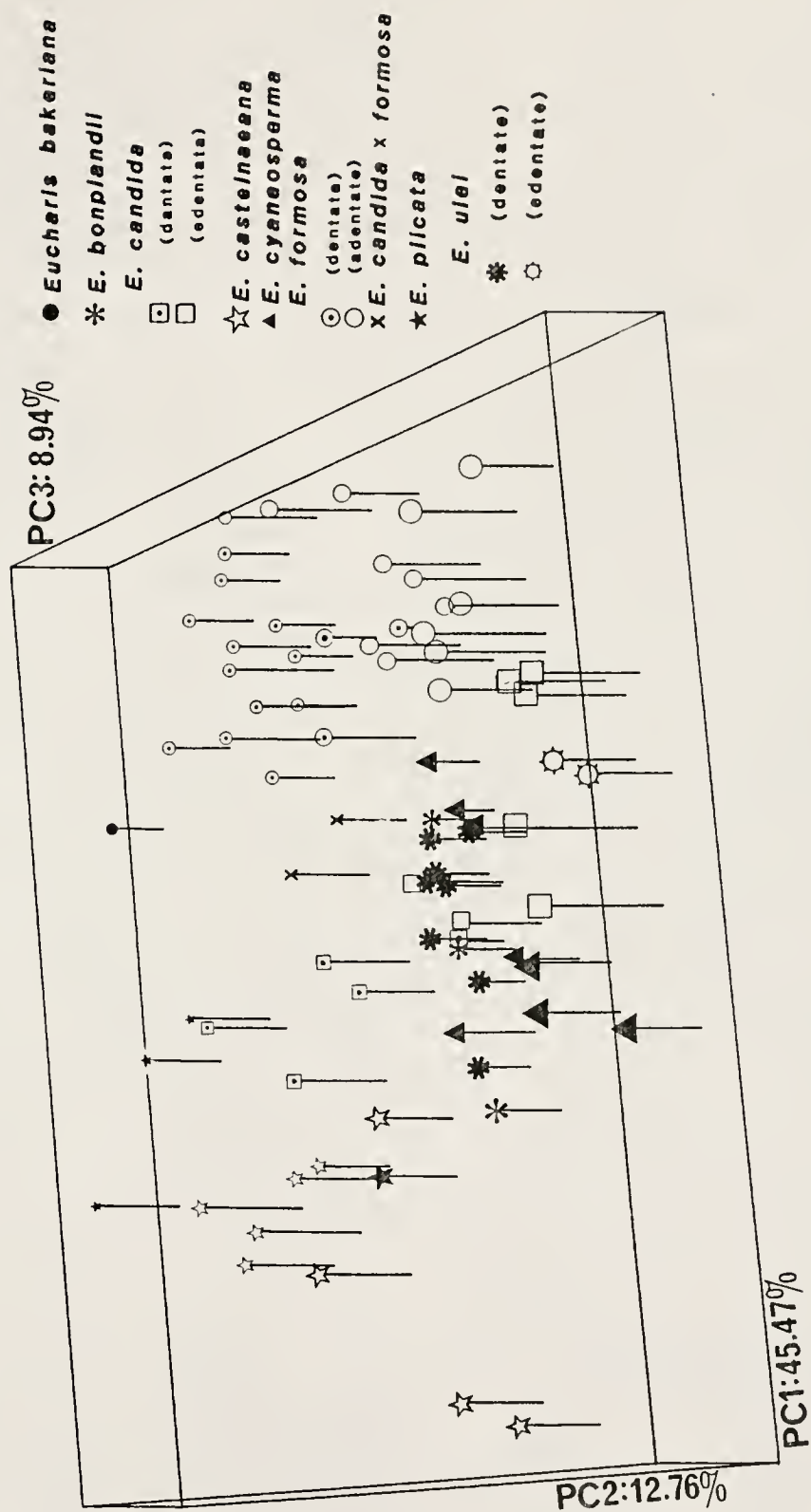


Figure 6.2. PCA scattergram based on variance across 15 floral characters in 78 OTU's representing Amazonian Eucharis (characters of staminal dentation removed).

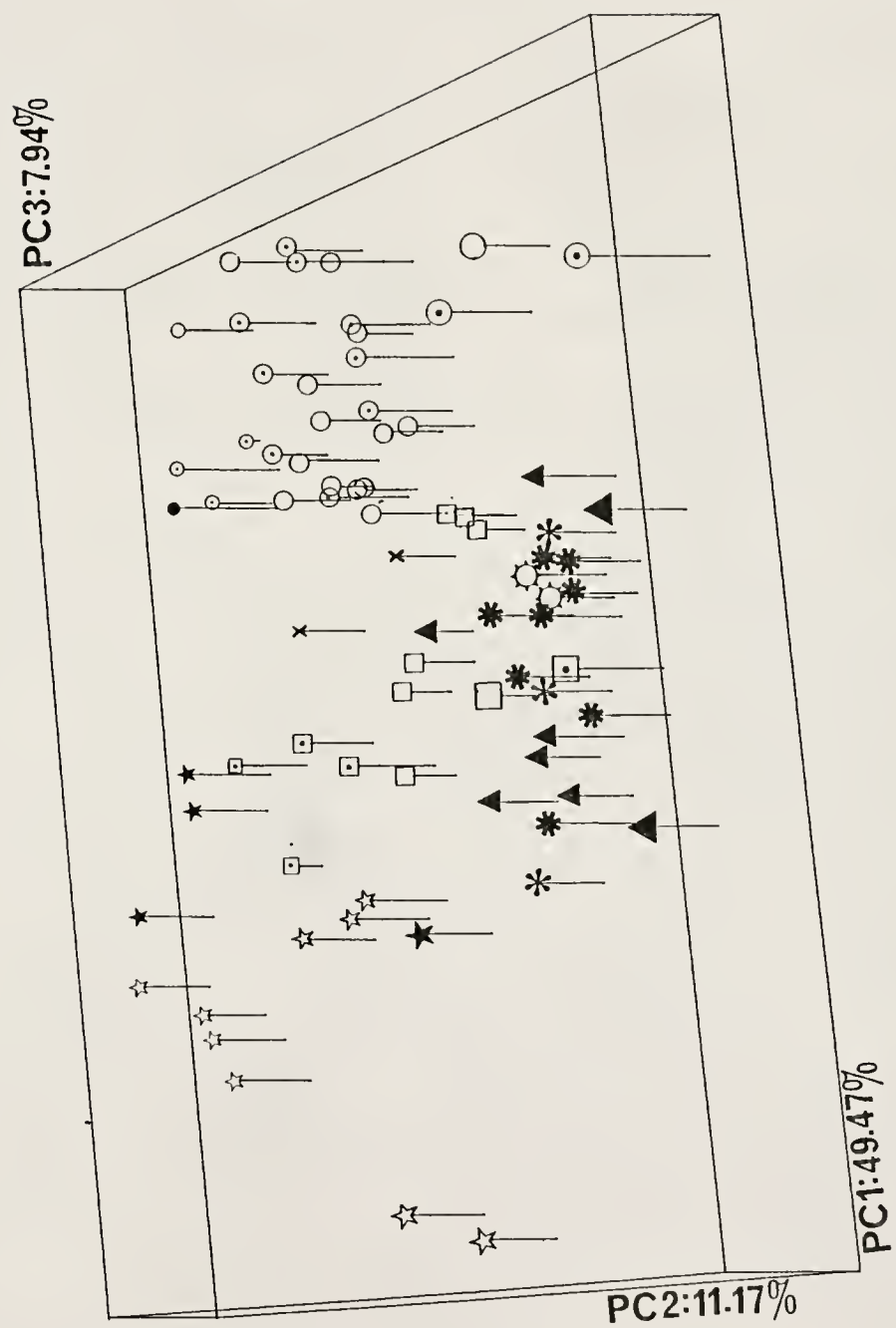




Figure 6.3. PCA scattergram based on variance across 8 androecial characters in 87 OTU's representing Amazonian Eucharis.

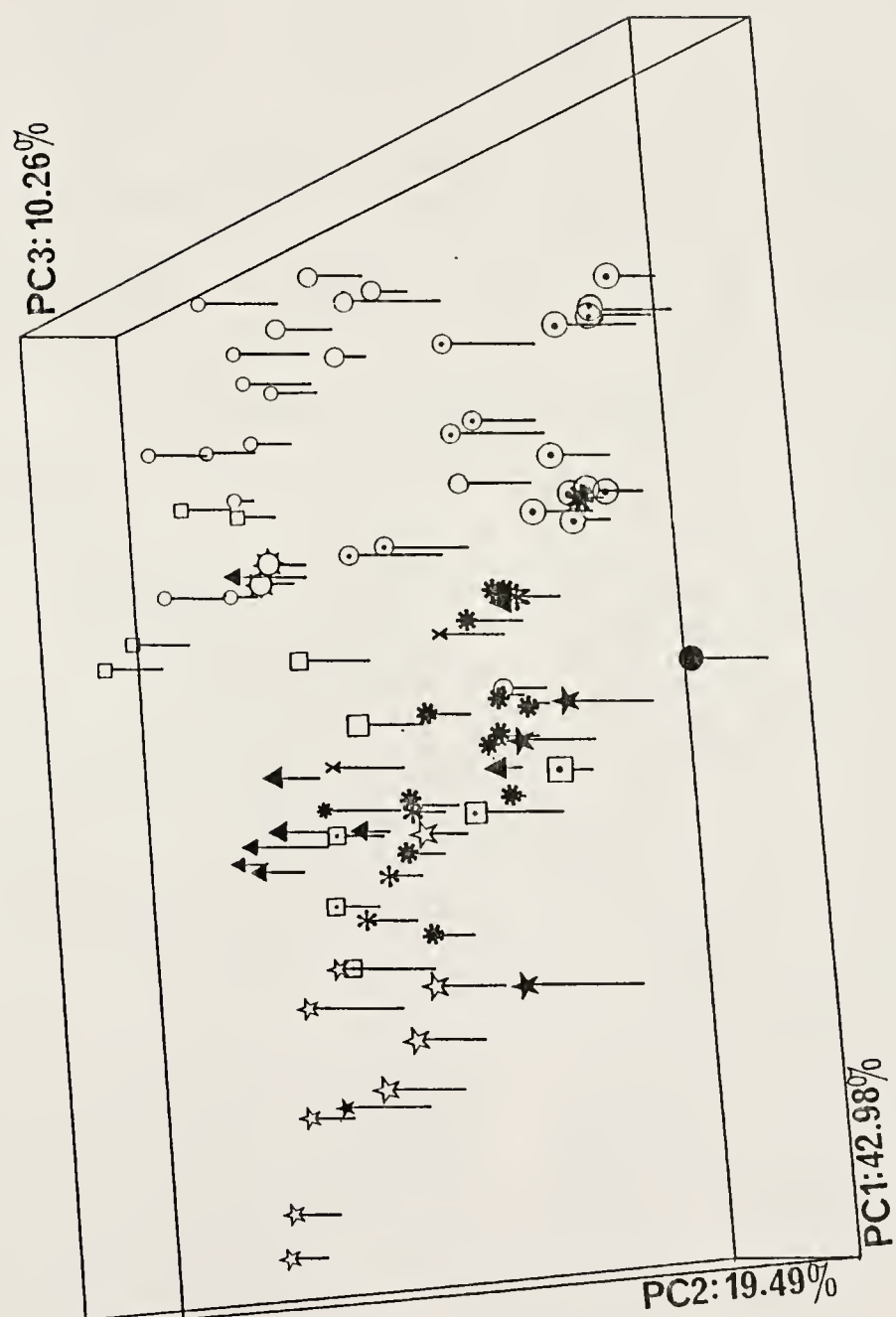


Figure 6.4. Cluster analysis dendrogram based on variance across 17  
floral characters in 78 OTU's representing Amazonian Eucharis.  
Refer to Appendix Table 1 for identification of OTU's.

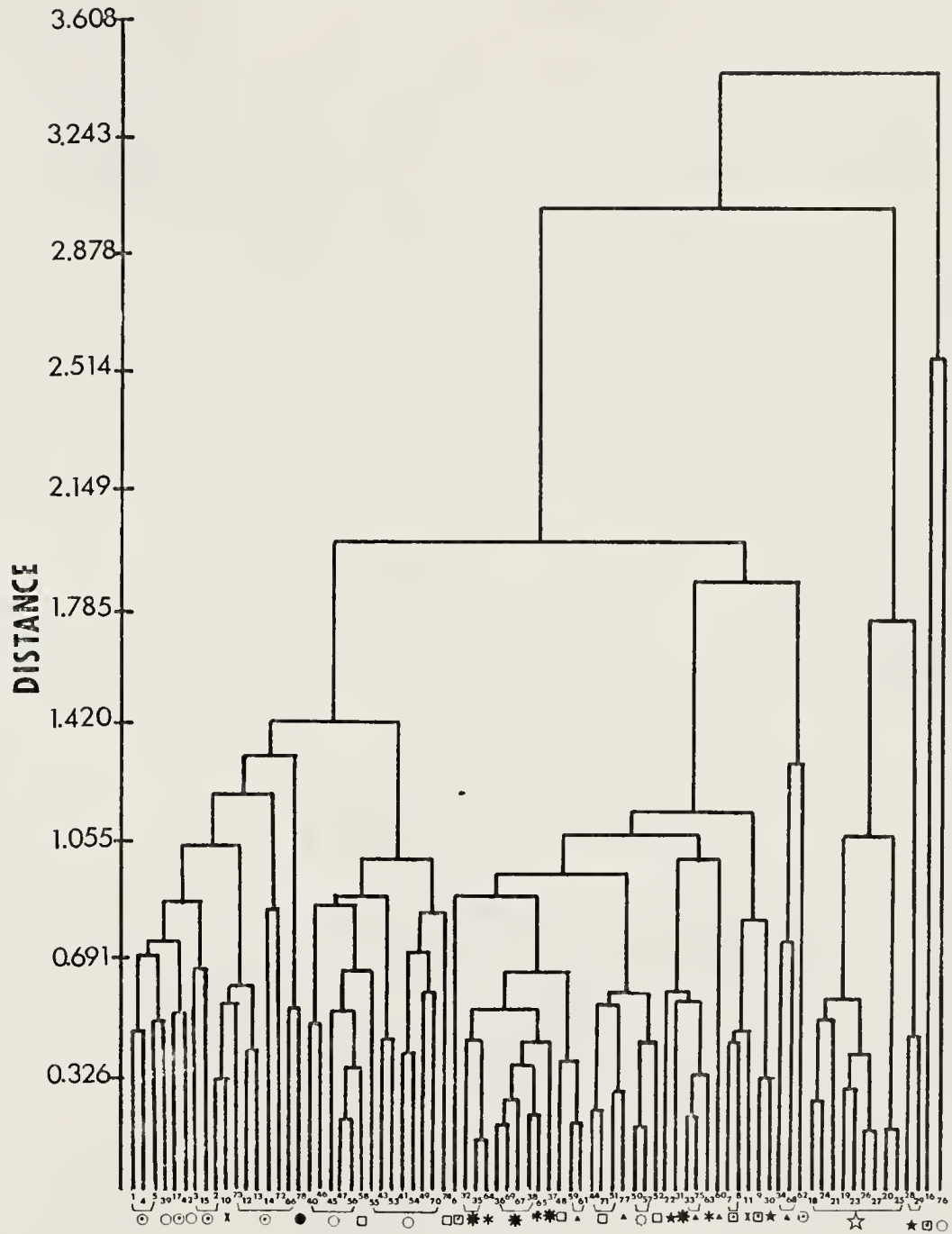


Figure 6.5. Cluster analysis dendrogram based on variance across 15 floral characters in 78 OTU's representing Amazonian Eucharis (characters of staminal dentation removed). Refer to Appendix Table 1 for identification of OTU's.





Figure 6.6. Cluster analysis dendrogram based on variance across 8  
staminal characters in 87 OTU's representing Amazonian Eucharis.  
Refer to Appendix Table 3 for identification of OTU's.

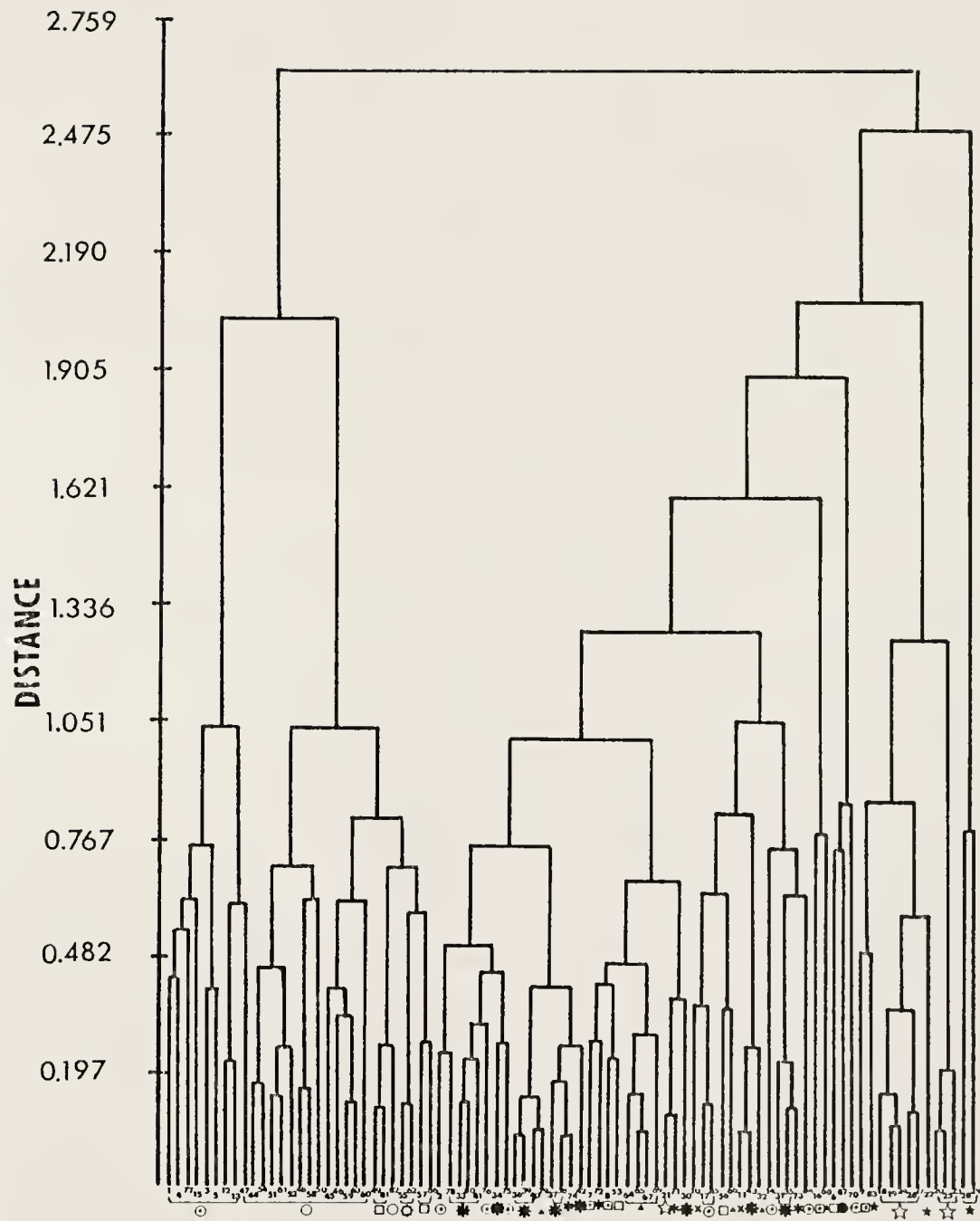


Figure 6.7. PCA scattergram based on variance across 17 floral characters in 28 OTU's representing Ecuadorian populations of *Eucharis candida* and *E. formosa*.

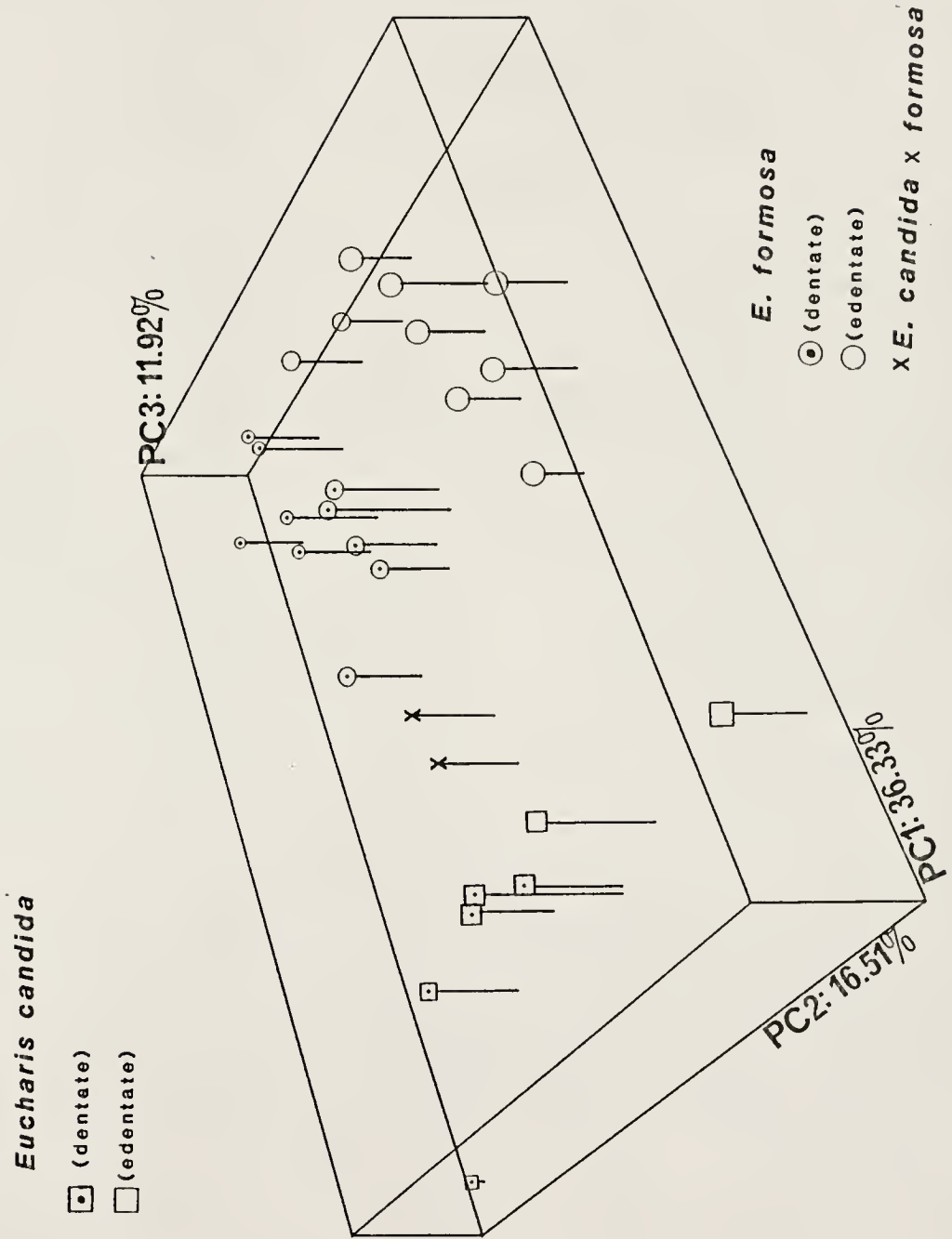


Figure 6.8. PCA scattergram based on variance across 15 floral characters in 28 OTU's representing Ecuadorian populations of *Eucharis candida* and *E. formosa* (characters of staminal dentation removed).

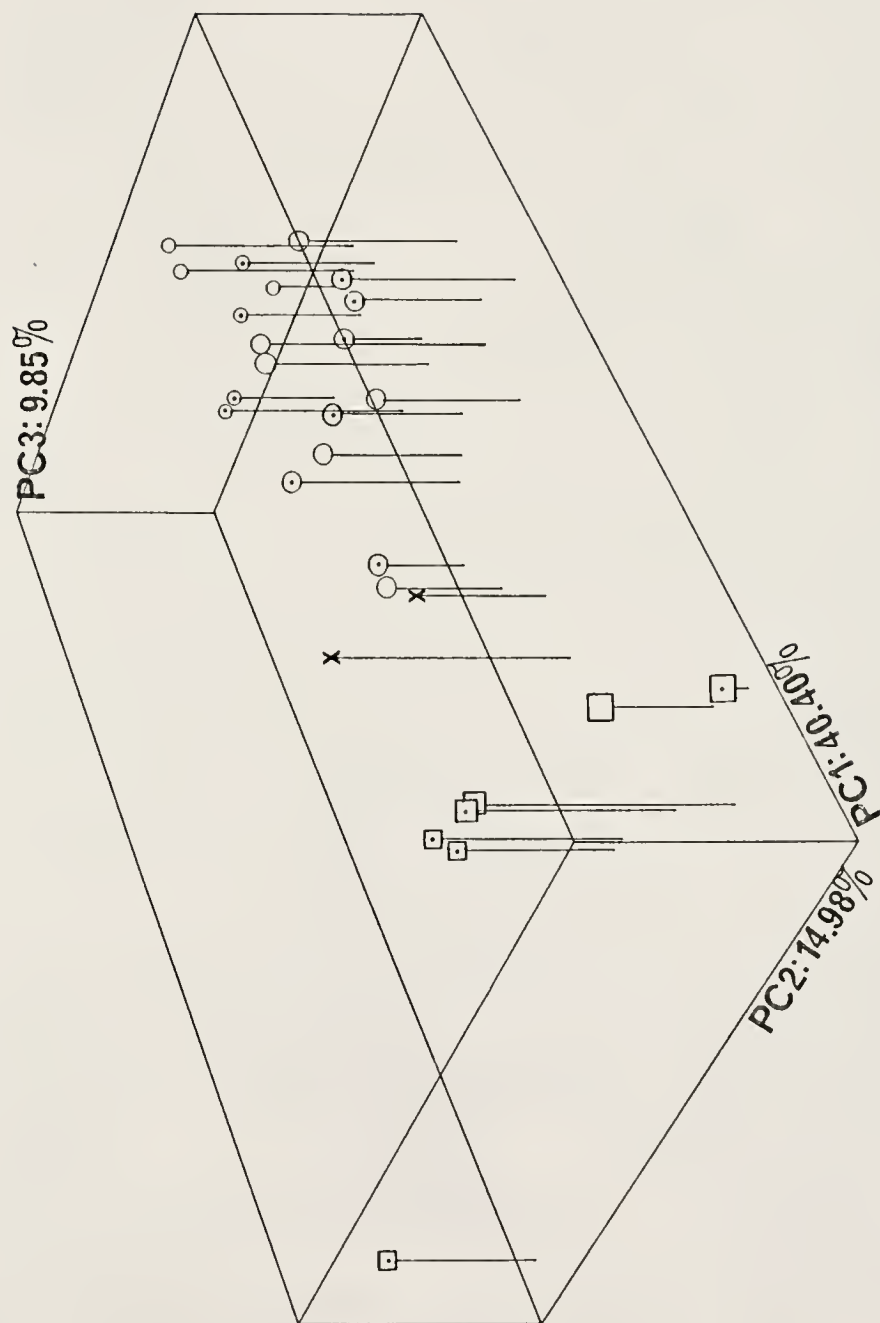




Figure 6.9. Cluster analysis dendrogram based on variance across 17 floral characters in in 28 OTU's representing Ecuadorean populations of Eucharis candida and E. formosa. Refer to Appendix Table 5 for identification of OTU's.

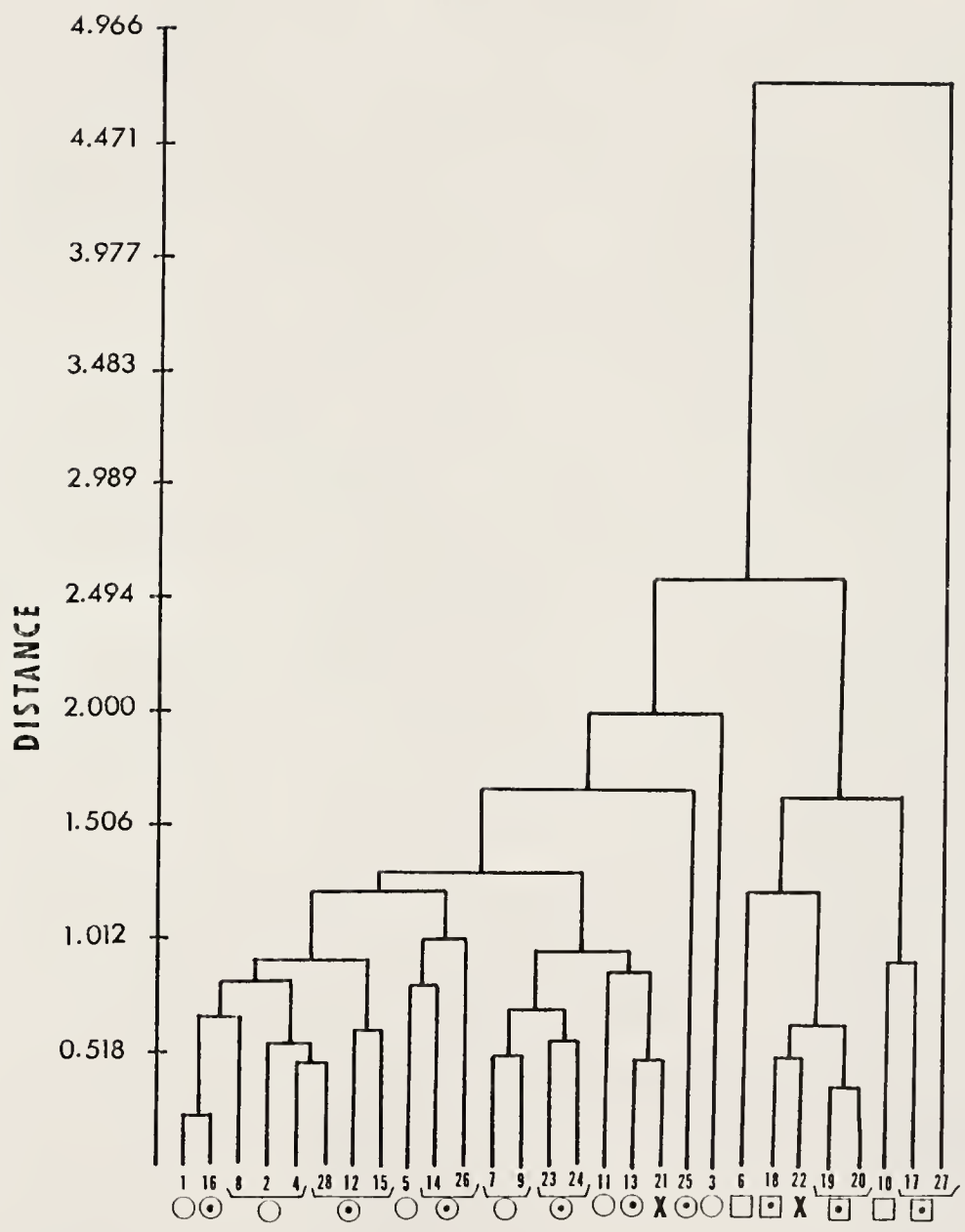


Figure 6.10. Cluster analysis dendrogram based on variance across 15 floral characters in 28 OTU's representing Ecuadorean populations of Eucharis candida and E. formosa (characters of staminal dentation removed). Refer to Appendix Table 5 for identification of OTU's.

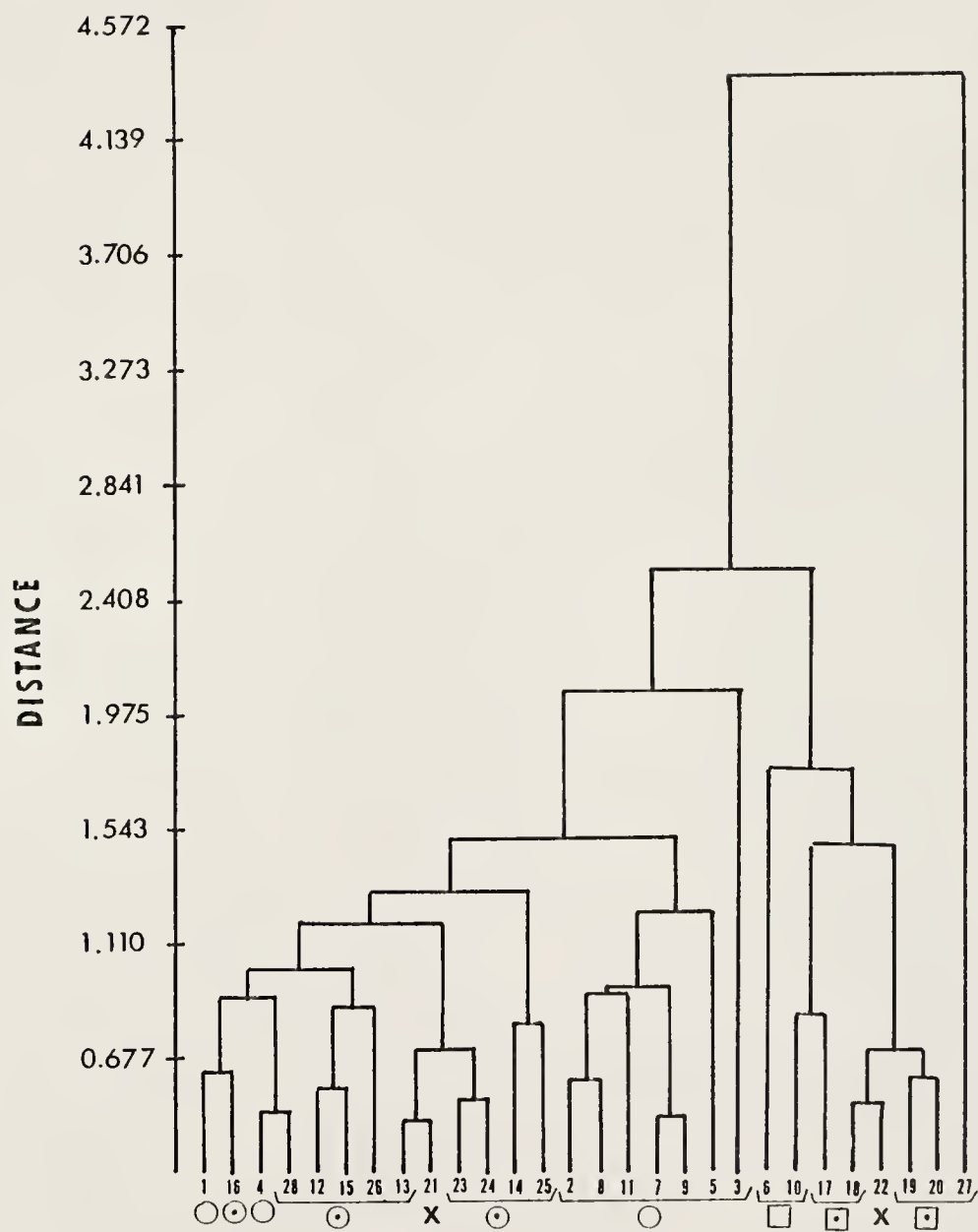


Figure 6.11. PCA scattergram based on variance across 17 floral characters in 20 OTU's representing Eucharis bouchei.

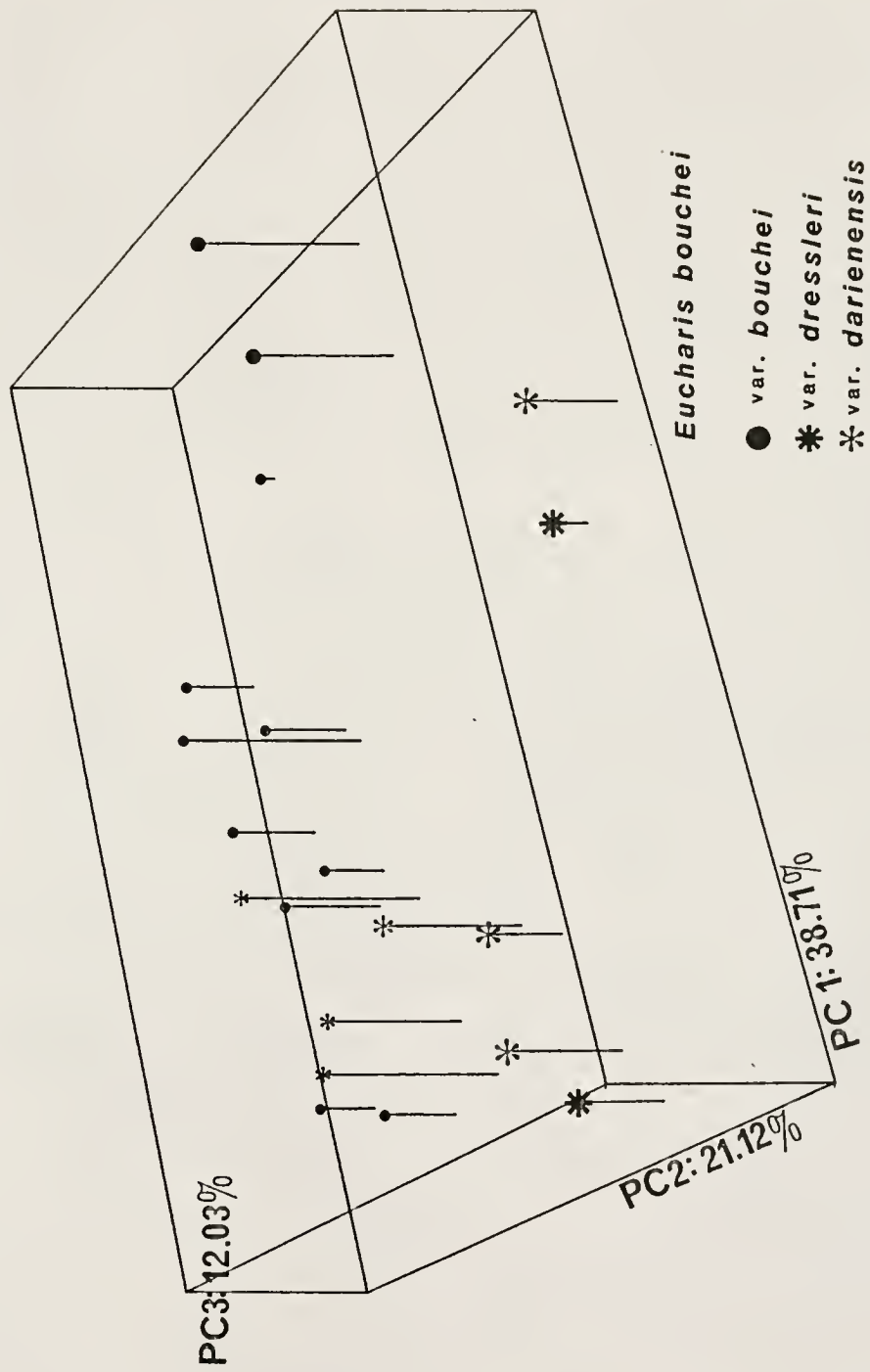




Figure 6.12. PCA scattergram based on variance across 17 floral characters in 20 OTU's representing Eucharis bouchei, with PC3 emphasized.

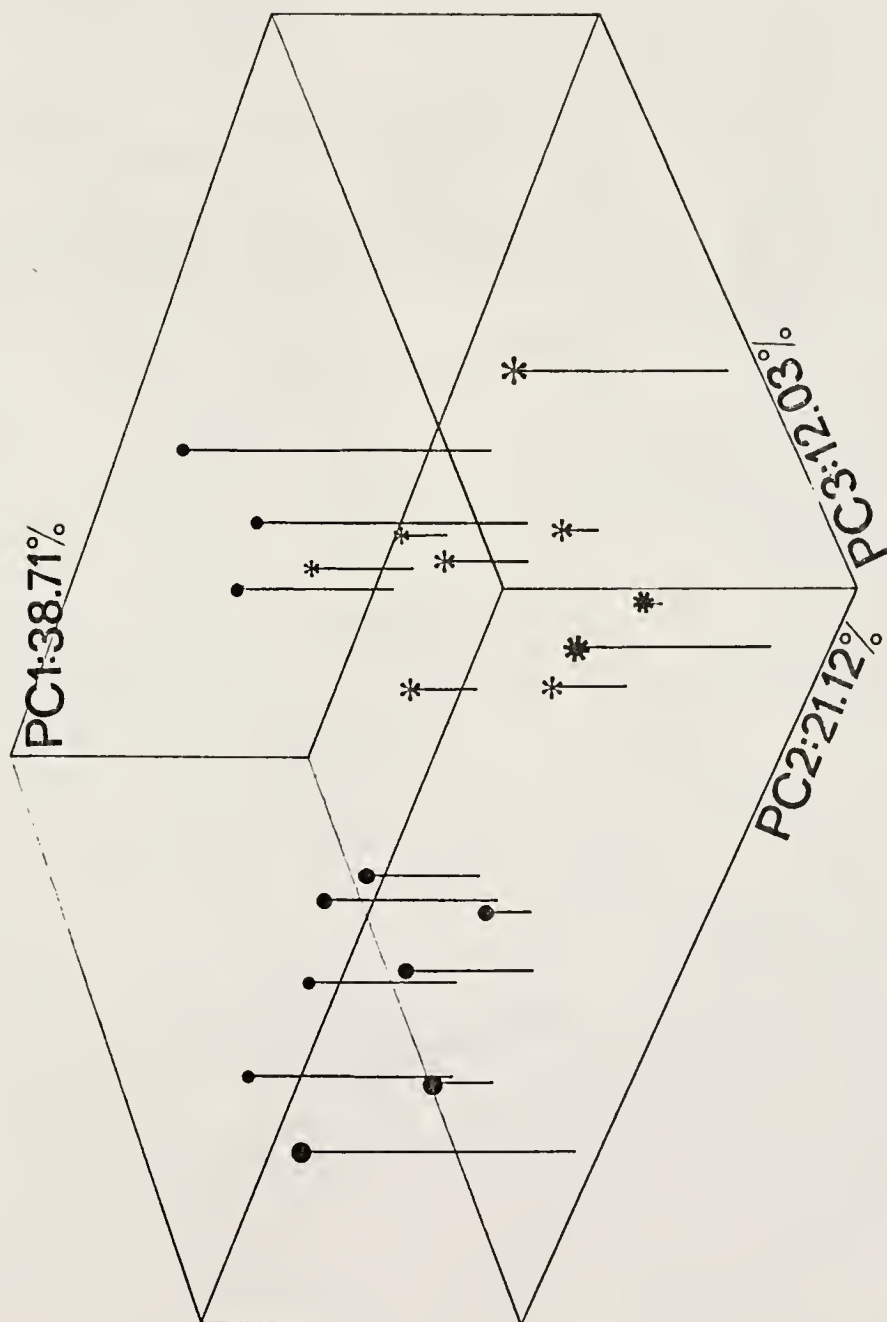
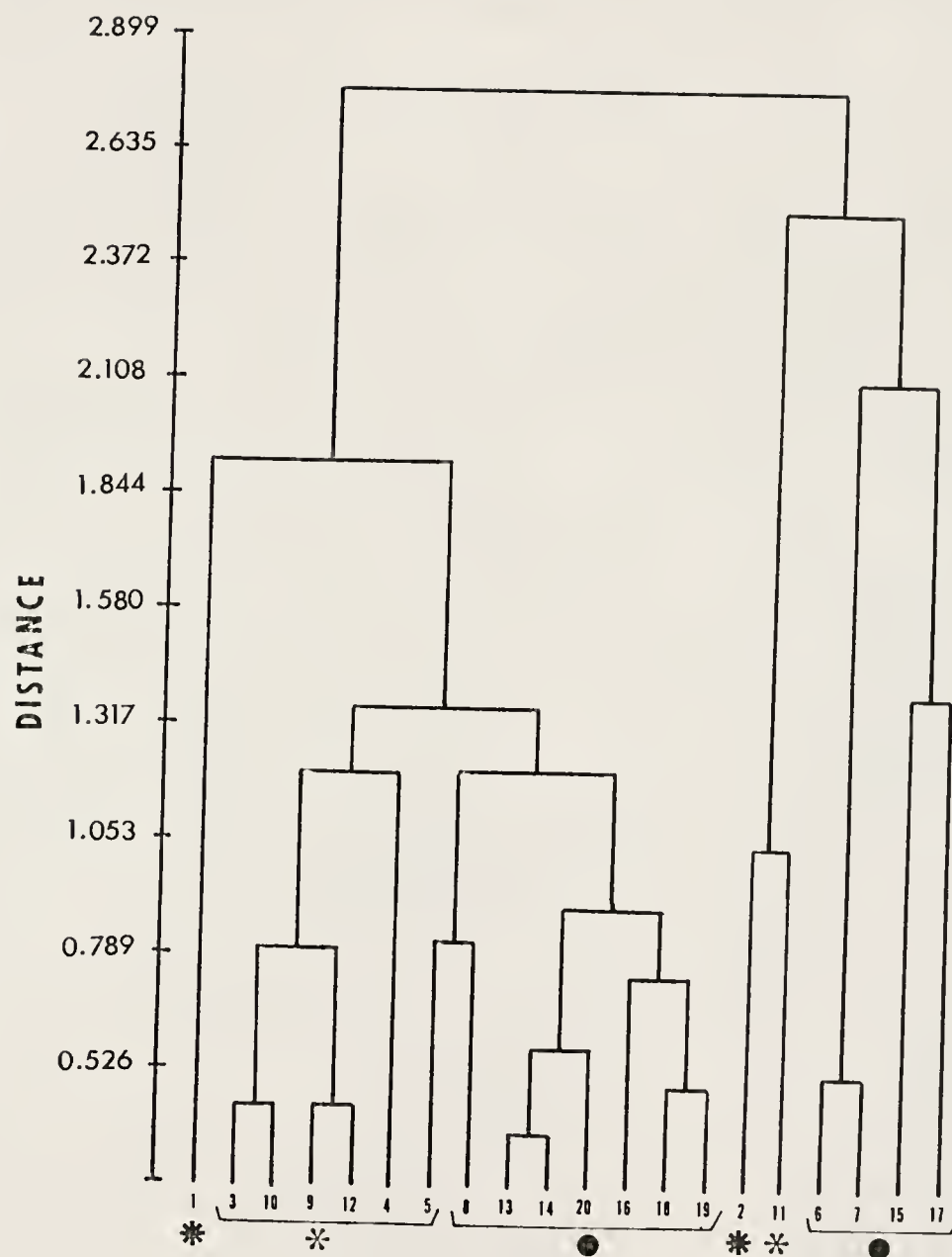


Figure 6.13. Cluster analysis dendrogram based on variance across 17  
floral characters in in 20 OTU's representing Eucharis bouchei.  
Refer to Appendix Table 7 for identification of OTU's.



## CHAPTER VII CHROMOSOME CYTOLOGY

Chromosome cytology of Amaryllidaceae has been a favored subject for investigation, chiefly due to the large size of the chromosomes and availability of material (Sharma and Bal, 1956). The subject has been reviewed by Flory (1977) and Meerow (1984). Mitotic studies have dominated the literature. *Microsporegensis* occurs completely inside the bulb when the inflorescence is nascent, and numerous bulbs must therefore be sacrificed for meiotic analysis without guarantee that necessary stages will be obtained (Nagalla, 1979; Ponamma, 1978; Williams, 1981).

Nonetheless, chromosome cytology of only a single species of Eucharis, E. amazonica, has been reported in the literature (Mookerjee, 1935; Nagalla, 1969; Sato, 1938). A large living collection of Eucharis and Caliphruria species has allowed a nearly complete investigation of somatic chromome cytology in the genus. The resulting data can be applied to problems of species delimitation in Eucharis and Caliphruria, as well as to wider questions of phylogenetic interest.

### Materials and Methods

Root tips were collected from living collections, pretreated for 2-3 hours at room temperature in 10 ppm solution of o-isopropyl-N-

phenylcarbamate (Storey and Mann, 1967), rinsed in distilled water, fixed in 3:1 mixture of 95% ETOH and chloroform (Carnoy's solution) at 18°C for 24 hr, then stored after fixation in 70% ETOH at 18°C. Root tips were hydrolyzed in 1N HCL at 50°C for 2-3 minutes, squashed, and stained with iron aceto-carmin. Only temporary slides were made. Metaphase configurations were photographed on a Nikon Labophot photomicroscope with AFX-II camera attachment, and haploid idiograms constructed from photomicrographs. Counts were made for a minimum of ten cells of each accession reported. Five metaphase configurations of each accession were analyzed morphologically for diploid species, two for tetraploids.

As absolute chromosome length can vary appreciably from cell to cell due to differential affects of pre-treatment (Tjio and Hagberg, 1951; Schlarbaum and Tsuchiya, 1984), relative length, based on a value of 100 for the haploid complement, was used to designate size class. Relative size classes are based on correlations between absolute size class [(modified from Battaglia (1955))] and relative length (RL) of mitotic metaphase preparations of various species of Eucharis, Eucrosia, Phaedranassa, and other Amaryllidaceae with  $2n = 46$ , all of which have similar relative length ranges.  $RL \geq 7.0$  = large, 5.0-7.0 = moderately large, 3.5-5.0 = medium,  $\leq 3.5$  = small. For tetraploid taxa, these values were halved. For the single, putatively triploid-derived species (E. amazonica), two-thirds of the diploid RL values were used to assign size class. Chromosome morphology, modified from Battaglia (1955), is defined as follows: metacentric, Arm Ratio (AR; long arm/short arm) = 1.00-1.10; near-metacentric, AR = 1.10-1.50; submetacentric, AR = 1.50-3.00; subtelocentric, AR = > 3.00.



Karyotype morphology was analyzed by Principle Component (PCA) and unweighted pairgroup cluster analysis (UPMGA of Sneath and Sokal, 1973) with CLUSTAN vers. 2.1 on the NERDC computer system of the University of Florida (see Chapter VI). Fifteen OTU's, representing non-hybrid, diploid taxa of Eucharis, Caliphruria, and Urceolina were analyzed for variance across thirteen characters. The characters were formed by nesting chromosome morphology within size classes (e.g., large/meta- or near-metacentric, large/submetacentric, etc.). Each OTU was then scored for the number of chromosomes within each nested group (refer to Table 1). For the purposes of these analyses, meta- and near metacentric morphologies were combined into a single category, as the distinction between these two categories is oftentimes slight and therefore most subject to error.

### Results

A somatic chromosome number of  $2n = 46$  is characteristic of Eucharis and Caliphruria, as well as the single species of Urceolina examined (Table 1). Two tetraploid species, E. bouchei from Central America, and E. bonplandii from Colombia, have  $2n = 92$ . Eucharis amazonica, with  $2n = 68$ , is the only known departure from these  $2n$  or  $4n$  karyotypes.

Karyotypes of all taxa studied are strongly bimodal (Figs. 1-25, Table 1). Approximately half the chromosomes are large to medium in size; the remainder are small. Mean numbers of chromosomes within each size class across all 12 diploid, non-hybrid, Eucharis and Caliphruria taxa examined are: large - 5.2 (SE 1.3), moderately large - 7.5 (SE

1.9), medium - 9.8 (SE 2.8), small - 23.5 (SE 2.7). If large and moderately large are combined into a single size class (large), all taxa (including both Urceolina microcrater) have either 12 or 14 large chromosomes.

In most species of Eucharis (Figs. 2, 4, 5, 6-12, 14, 18-20, 22C-E, 23, 24A, C, 25C, D, F), the two largest chromosome pairs are metacentric or near-metacentric. In a single species, E. astrophiala (Figs. 1, 22A), the largest pair is submetacentric, as is the case in Urceolina microcrater (Fig. 26). The second largest pair of E. astrophiala is subtelocentric. This species is a peripheral isolate of subg. Eucharis, the only species of this subgenus on the western Andean slopes south of Colombia. It has uniquely bullate-pustulate leaf morphology, and the largest pollen grain in the genus. Caliphruria subedentata is heteromorphic for the largest chromosome pair (Figs. 16, 25A). One of the homologs is metacentric, while the other is submetacentric. Five different collections of this species all exhibit this heteromorphism. Pollen of this species stains only 65-75% with Alexander's (1969) stain, which may be a consequence of this heteromorphism. The second largest chromosome pair of X Calicharis butcheri, putatively an intergeneric hybrid between E. sanderi and C. subedentata, is submetacentric, and may conceivably be homologous to the submetacentric member of the largest pair in C. subedentata.

The second largest chromosome pair is also submetacentric in a few species of Eucharis and Caliphruria: E. bakeriana (Figs. 3, 22B), some populations of E. bouchei (Figs. 13, 24B), E. bonplandii (Figs. 15, 24C), and C. korsakoffii (Figs. 17, 25B).

Telocentric chromosomes were observed in only two species, E. anomala (subg. Heterocharis, Figs. 18, 25C), and E. castelnaeana (subg. Eucharis, Figs. 4, 22D). The number of subtelocentric chromosomes, however, is a major source of karyotypic variation among the species.

Secondary constrictions were resolved only in a single chromosome of E. bakeriana (subg. Eucharis, Figs. 3, 22B), and four chromosomes of E. amazonica (subg. Heterocharis, Figs. 19, 25F). Terminal satellites were not resolved in any species examined, even though Mookerjee (1955), Nagalla (1969) and Sato (1938) all reported their occurrence in E. amazonica. Mitotic metaphase configurations of cultivated material (received without provenance) of E. amazonica did resolve several SAT-chromosomes, however. In new collections from Peru, from which karyotypes reported here were prepared, satellites were not apparent.

Tetraploidy in Eucharis is limited to two species, E. bonplandii, a rare Colombian species, and E. bouchei from Central America. Karyotypically, the tetraploid Eucharis species are considerably heteromorphic (Fig. 24). Karyotypes of two geographically isolated and morphologically distinct populations of E. bouchei var. bouchei (Figs. 13-14, 24A-B; Table 1) are quite different. Eucharis bouchei var. dressleri is an unstable tetraploid (Figs. 11-12, 24C). Fifteen percent of all root cells from which metaphase counts were obtained had 46 chromosomes.

#### Phenetic analyses of karyotype variation

PCA. Ordination of 15 diploid karyotypes by principle components resolved almost 70% of total variance in the first three principle components. By exploring the variance components of each of the three

PC's (Table 2), it is possible to determine which categories of chromosome morphology are the most variable. From this, one can perhaps infer the patterns of karyotypic change that has occurred among species and between genera. Characters 2 (large/submetacentric), 5 (moderately large/submetacentric) 9 (medium/subtelocentric), and 15 (small/subtelocentric) were the most important contributors to total variance of PC1. Characters 3 (large/subtelocentric), 4 (moderately large/metacentric), 5, and 11 (small/submetacentric) are largely represented in PC2. PC3 is weighted for characters 4, 6 (moderately large/subtelocentric), 7 (medium/metacentric) and 10 (small/metacentric).

Ordination by the first three PC's produces the scattergram in Fig. 27. Along PC1, the component of greatest variance, almost all the karyotypes are found in the same general area of the scattergram, indicating that in terms of chromosome categories large-submetacentric, moderately large-submetacentric, medium-subtelocentric, and small-subtelocentric, the taxa do not vary appreciably from each other. A notable exception is E. bakeriana. This species has 10 moderately large-subtelocentric chromosomes (six is the highest number to occur in all other taxa analyzed), and the only species to have any small-subtelocentric chromosomes.

Greatest phenetic differentiation in karyotype occurs along PC2. Eucharis astrophiala is the most isolated taxon along this component. This species has the largest number of moderately large-submetacentric chromosomes (10), the category which contributed the greatest variance to PC2. Eight taxa (E. anomala, E. bouchei var. dressleri, E. castelnaeana, E. cyaneosperma, E. formosa from Ecuador, E. ulei, C.

subedentata, and Urceolina microcrater) form a relatively distinct phenetic group along PC2. The similarity of karyotype of the sibling species E. cyaneosperma and E. ulei is evident by their close proximity in the scattergram. The remaining taxa in this phenetic group are a heterogeneous assemblage of widely related species. Eucharis anomala and E. castelnaeana separate from all other taxa along PC3 on the basis of their two, small, telocentric chromosomes. The remaining taxa (E. candida, E. formosa from Peru, E. plicata and C. korsakoffii) are united along PC2 but separate along the length of PC1. The karyotype relationship of both subspecies of E. plicata (Figs. 8-10, 23C-D; table 1) is evident by their proximity in the scattergram. The karyotype divergence of Peruvian E. formosa from Ecuadorean populations is evident as well by the distance between these two karyotypes in the scattergram.

Cluster analysis. The dendrogram generated by the UPGMA algorithm (Fig. 28) supports many of the results of PCA. The karyotype of E. bakeriana is a distant outlyer to all other OTU's, fusing with the rest of the group at a distance coefficient (DC) of 4.408. Eucharis astrophiala is also an outlyer, but at a DC of only 2.630. Other than these two OTU's, three main clusters are formed in the dendrogram. The two populations of E. formosa do form a cluster at DC 0.363, but not until after the two subspecies of E. plicata join with Peruvian E. formosa. Eucharis ulei and its sibling species E. cyaneosperma join at a DC of only 0.131. The diploid karyotype of E. bouchei var. dressleri joins this cluster at DC 0.822. Caliphruria korsakoffii and Urceolina microcrater fuse at a DC 0.509. Caliphruria subedentata is an outlyer to this center cluster. The third cluster is a heterogeneous one. Eucharis anomala and E. castelnaeana fuse at a relatively high DC of



1.252, probably more on the basis of their small-telocentric chromosomes than any other feature of their karyotypes. Eucharis candida joins them at a DC of 1.602.

### Discussion and Conclusions

A somatic chromosome number of  $2n = 46$  (or derivations thereof) is characteristic of most genera of neotropical Pancratioidinae (Di Fulvio, 1972; Flory, 1977; Meerow, unpubl. data; Williams, 1981). All paleotropical genera have  $2n = 22$  or 20 (Meerow, unpubl. data; Ponnammma, 1972; Zaman and Chakraborty, 1974). This suggests a polyploid origin for the neotropical genera of the infrafamily from an ancestor with  $2n = 22$  (cf. Pancratium L.) via chromosome fragmentation and subsequent doubling (Lakshmi 1978; Sato 1938). The most common base number occurring in the Amaryllidaceae is  $x = 11$  (Flory, 1977; Goldblatt, 1976; Traub, 1963), and  $2n = 22$  characterizes many widely unrelated genera.

Two major trends characterize amaryllidaceous karyotype evolution (Meerow, 1984). Certain genera exhibit great karyotypic stability, with low frequency of polyploidy [(e.g., Crinum L. (Jones and Smith, 1967; Raina, 1978); Hippeastrum Herbert (Naranjo and Andrada, 1975)]. Similar chromosome morphology among the species of such genera is characteristic. Their polyploids tend to be autopolyploid in origin. At the other extreme, a genus may exhibit great variation in both chromosome number and morphology [e.g., Hymenocallis Salisb. (Flory, 1976; Flory and Schmidhauser, 1957; Lakshmi, 1978); Lycoris Herbert (Inariyama, 1931, 1933, 1937, 1953; Bose and Flory, 1963)]. In such



genera, allopolyploidy has been implicated as an important factor in speciation.

Eucharis and related genera are somewhat intermediate between these two extremes. Chromosome number is very stable in Eucharis, and incidences of polyploidy are low. The origins of the polyploids (i.e., whether auto- or allopolyploid) are inconclusive (attempts to secure meiotic figures have been unsuccessful). But changes in chromosome morphology among the species has been extensive enough that a general karyotypic formula cannot be constructed, as has been done for Crinum (Jones and Smith, 1967; Raina, 1978) and Hippeastrum (Naranjo and Andrada, 1975).

Chromosomal symmetry has classically been cited as evidence of karyotypic evolution (Levitsky, 1931; Stebbins, 1950), i.e., karyotype of greatest symmetry in a particular phylogeny is the most primitive, and that of least symmetry, the more derived. Jones (1978) has challenged this tenet, though the evidence for the reverse process is inextricably linked to accompanying changes in chromosome number [i.e., Robertsonian changes (Robertson, 1916)]. Centric fusion and centric fission have respectively been implicated in the evolution of Lycoris (reviewed by Jones, 1978) and Hymenocallis (Flory, 1976). In Eucharis and Caliphruria, no such change in number is in evidence. Thus, pericentric inversion, centric shift, or unequal translocations (Grant, 1975; Jackson, 1971) would be the most likely causative factors generating transformations in chromosome morphology of Eucharis and Caliphruria.

Morphological change in the largest chromosome pair in Eucharis and related genera is rare, but in both cases (Eucharis astrophiala and

Urceolina microcrater), large-scale phenetic divergence is correlated with such change, in one case at the generic level.

Slightly more common (4 taxa) is the change in the second largest chromosome pair, from metacentric to submetacentric. Again, a level of morphological divergence correlates in these taxa (E. bonplandii, E. bouchei, E. bakeriana, and C. korsakoffii). The case of E. bakeriana is particularly interesting. This rare species occurs in the same area as some Peruvian populations of E. formosa. A measure of karyotypic relationship between these two species in Peru may be the moderately large subtelocentric chromosome (no. 9 in Figs. 22B and 23B) with a very short arm. Except for the submetacentric second-largest pair in E. bakeriana (along with generally increased asymmetry), these two karyotypes are very similar. The species are cladistically very close as well (see Chapter IX). Eucharis bakeriana may represent a case of rapid phenetic divergence via chromosomal change.

The large, heterogenous group in the scattergram (Fig. 27) may represent taxa with more ancestral karyotype morphology (i.e., more symmetrical), since it includes taxa of different genera as well as Eucharis species. The putatively most primitive species of Eucharis, E. anomala, is included within this group. Number of subtelocentric chromosomes is the best indicator of symmetry variance in Eucharis karyotypes, and these taxa do have the lowest numbers of subtelocentrics (2-6). Among the karyotypes of this group, the large chromosome size class and the metacentric subclass of moderately large chromosomes show the least variance (Table 1). Enough variance is expressed in all other categories to make generation of a karyotype formula for Eucharis difficult.

Karyotypes of Caliphruria korsakoffii and Urceolina microcrater appear to have some phenetic similarity, on the basis of cluster analysis (Fig. 28). This is all the more interesting due to the fact that C. korsakoffii is the only species of Caliphruria found in Peru. Urceolina is completely endemic to Peru. Since both are divergent taxa, I would suspect that karyological features common to both species represent symplesiomorphies.

The presence of telocentric chromosomes in both E. anomala and E. castelnaeana are probably independent occurrences, considering the phenetic and cladistic distance between these species. The presence of telocentrics, however, correlates with green, thin-walled fruits in both species.

Eucharis amazonica, with  $2n = 68$ , is an unusual species. Known in the wild only from the Huallaga valley of Peru, E. amazonica has never been collected in fruit, and will not set capsules with self, sibling, or interspecific pollen. Pollen stains only 50-65% with Alexander's (1969) stain. On the basis of meiotic study, Nagalla (1979) considered E. amazonica an aneuploid with a  $6x + 2$  constitution. At metaphase I she observed 873 univalents, 325 bivalents, 61 trivalents, 61 quadrivalents, 30 pentavalents, and 45 hexavalents in the 35 cells analyzed. Occurrence of bridge fragment configurations at anaphase I suggested inversion heterozygosity. Nagalla (1979) concluded that the species is a segmental allo-hexaaneuploid. I believe E. amazonica is a triploid derived isolate of the genus ( $3x - 1$ ), with many ancestral (or derived, in the case of secondary petiolar bundles) characters shared with E. anomala. A similar case has occurred in Eucrosia (Meerow, 1987), another Andean genus of pancratioid Amaryllidaceae. Eucrosia bicolor

Ker Gawler has  $2n = 68$  (the rest of the genus has  $2n = 46$ ). In E. bicolor, however, pollen stainability is not reduced, and plants have been collected in fruit.

Eucharis bouchei var. dressleri is an unstable tetraploid. Somatic cells of the root tips have both tetraploid (92) and diploid (46) counts. Snoad (1955) reported karotype instability in Hymenocallis narcissiflora, but aneuploid numbers as well as polyploid counts were observed in the cells of the latter species.

Polyploid species of Eucharis do not show any marked effects of increased chromosome number beyond an increase in size of root cells, and a slight thickening of the leaf laminae. Eucharis bonplandii, in addition, develops a glaucous bloom on the leaves in strong light. Tetraploidy may, however, have aided the successful colonization of Central America by the E. bouchei complex (cf. Stebbins, 1985; see Chapter IX).

Patterns of chromosomal variation (Figs. 27-28) confirm patterns of phenetic variation (Chapter VI) and cladistic relationship (Chapter XI). Karyotypes of E. plicata, and sibling species E. ulei and E. cyaneosperma respectively, are very similar. Cluster analysis indicates that the karyotypes of E. bouchei, E. cyaneosperma and E. ulei are similar. Cladistic analysis indicates that these three taxa comprise a monophyletic group. Karyotype divergence is evident between E. candida and E. formosa, mirroring morphological divergence (Chapter VI). Isozyme variation (Chapter VIII), however, obscures the relationship between these two sibling species.

In conclusion, karyotype diversity has undoubtedly contributed to species and generic divergence in Eucharis, Caliphruria, and Urceolina.

Chromosomal change has not been through dramatic reorganization of the genome through Robertsonian changes, but probably via non-reciprocal interchanges between chromosomes, infra-chromosomal structural change, and mutation. Evidence of mutation is the presence of rare alleles in all species complexes that have been electrophoretically analyzed (Chapter VIII). In some cases, rapid, sympatric speciation may have been facilitated by chromosomal structural change.

Table 7.1. Karyotype data, Eucharis, Caliphruria, and Urceolina. All vouchers deposited at FLAS unless otherwise stated.

TAXON, VOUCHER, & FIG. NO.	CHROMOSOME NUMBER	CHROMOSOME RANGE (relative length) <sup>a</sup>	CHROMOSOME SIZE <sup>b</sup> GROUPS			CHROMOSOME <sup>c</sup> MORPHOLOGY			OTU NO. & LABEL FOR PCA & CLUSTER ANALYSIS		
			L	ML	M	S	L	ML	M	S	
<u>EUCCHARIS SUBG. EUCCHARIS</u>											
<u>E. astrophiala</u>	46	2.05 - 8.27	4	8	10	24	m:		6		9, ASTRO
( <u>Meerow 1111</u> )							nm:		10		
Figs. 1, 22A							sm:	2	6	10	8
							st:	2	2		
<u>E. candida</u>	46	1.93 - 9.69	8	4	8	26	m:	2		8	2, CAND
( <u>Schunke 14155B</u> )							nm:	2		2	14
Figs. 2, 22B							sm:	2		6	4
							st:	2	4		
<u>E. bakeriana</u>	46	1.71 - 10.53	4	10	10	22	m:	2			13, BAK
( <u>Meerow 1108</u> )							nm:		2	6	
Figs. 3, 22C							sm:	2		4	16
							st:		10	4	



Table 7.1--continued.

TAXON, & VOUCHER, & FIG. NO.	CHROMOSOME NUMBER	CHROMOSOME SIZE RANGE (relative length) <sup>a</sup>	CHROMOSOME SIZE <sup>b</sup> GROUPS		CHROMOSOME <sup>c</sup> MORPHOLOGY		OTU NO. & LABEL FOR PCA & CLUSTER ANALYSIS
			L / ML / M / S	L / ML / M / S	L / ML / M / S	L / ML / M / S	
<u>E. castelnaeana</u>	46	2.04 - 11.45	4	8 12 22	m:	4	3, CAST
( <u>Schunke 14156</u> )					nm:	4 2 14	
Figs. 4, 22D					sm:	4 10 2	
					st:	4	
					t:	2	
<u>E. cyaneosperma</u>	46	2.27 - 9.48	6	6 14 20	m:	2 2 6	8, CYAN
( <u>Meerow 1032</u> )					nm:	2 2 6 6	
Figs. 5, 22E					sm:	2 2 6 8	
					st:	2	
<u>E. formosa</u>	46	2.12 - 11.10	6	6 10 24	m:	4	1, FORM-P
( <u>Schunke 14174</u> )					nm:	14	
Figs. 6, 23B					sm:	2 4 6	
					st:	6 6	



Table 7.1--continued.

TAXON, & VOUCHER, & FIG. NO.	CHROMOSOME NUMBER	CHROMOSOME RANGE (relative length) <sup>a</sup>	CHROMOSOME SIZE <sup>b</sup> GROUPS			CHROMOSOME <sup>c</sup> MORPHOLOGY			OTU NO. & LABEL FOR PCA & CLUSTER ANALYSIS
			L / ML / M / S	L	ML / M / S	L / ML / M / S	L	ML / M / S	
<u>E. ulei</u>	46	2.18 - 9.60	6	6	12 22	m:	2	2	4, ULEI
(Schunke 14153)						nm:	4	6	14
Figs. 9, 23E						sm:	2	2	2
						st:	2		6
<u>E. bouchei</u> var.	46, 92	2.07 - 9.63	4	10	14 18	m:	4	2	15, BOUCHEI
<u>dressleri</u> <sup>d</sup>						nm:		6	10
(Meerow 1107)						sm:	4	6	8
Figs. 11-12, 24C						st:	6		
<u>E. bouchei</u> var.	92	0.54 - 5.27	14	16	14 48	m:			2
<u>bouchei</u>						nm:	2	2	18
(Meerow 1157)						sm:	10	6	28
Figs. 13, 24B						st:	2	10	6

Table 7.1--continued.

TAXON, VOUCHER, & FIG. NO.	CHROMOSOME NUMBER	CHROMOSOME SIZE RANGE (relative length) <sup>a</sup>	CHROMOSOME SIZE <sup>b</sup> GROUPS		CHROMOSOME <sup>c</sup> MORPHOLOGY		OTU NO. & LABEL FOR PCA & CLUSTER ANALYSIS
			L / ML	M / S	L / ML	M / S	
<u>E. bouchei</u> var.	92	0.85 - 4.54	10	18 16 48	m: 2 2	4 4	6
<u>bouchei</u>					nm: 2	6	28
( <u>Meerow 1125</u> )					sm: 6	8 4	14
Figs. 14, 24A					st: 8	2	
<u>E. bonplandii</u>	92	0.95 - 4.82	14	12 24 42	m: 6	6	18
( <u>Bauml 686, HUNT</u> )					nm: 2	4 16	18
Figs. 15, 24D					st: 6	8 2	
<u>EUCHARIS SUBG. HETEROCHARIS</u>							
<u>E. anomala</u>	46	2.13 - 10.87	6	8 6 26	m: 4	2	10, ANOMALA
( <u>Meerow 1141</u> )					nm: 2	18	
Figs. 18, 25C					sm: 6	6 6	6
					st: 2	2	

Table 7.1--continued.

TAXON, & VOUCHER, & FIG. NO.	CHROMOSOME NUMBER	CHROMOSOME RANGE (relative length) <sup>a</sup>	CHROMOSOME SIZE <sup>b</sup> GROUPS			CHROMOSOME <sup>c</sup> MORPHOLOGY			OTU NO. & LABEL FOR PCA & CLUSTER ANALYSIS
			L / ML	M	S	L	ML	M / S	
<u>E. amazonica</u>	68	1.37 - 7.00	10	10	12	36	m: 2	2	2
(Schunke 14179)							nm: 4		16
Figs. 19, 25F							sm: 2	2	2
							st: 4	6	10
<u>E. X grandiflora</u>	46	2.24 - 9.17	8	4	8	26	m: 2		2
(Meerow 1104)							nm: 2		2
							sm: 2	2	4
Figs. 20, 25D							st: 2	2	2
<u>X Calicharis</u>	46	2.24 - 10.47	6	6	16	18	m: 2		
<u>butcheri</u>							nm: 2	2	6
(Meerow 1110)							sm: 2	4	8
Figs. 21, 25E							st: 2		2

Table 7.1--continued.

TAXON, VOUCHER, & FIG. NO.	CHROMOSOME NUMBER	CHROMOSOME SIZE RANGE (relative length) <sup>a</sup>	CHROMOSOME SIZE <sup>b</sup> GROUPS		CHROMOSOME <sup>c</sup> MORPHOLOGY		OTU NO. & LABEL FOR PCA & CLUSTER ANALYSIS
			L / ML / M / S	L / ML / M / S	L / ML / M / S	L / ML / M / S	
<u>CALIPHRURIA</u>							
<u>C. korsakoffii</u>	46	2.16 - 10.16	8	4 10 24	m: 2	2 2	7, KORS
(Meerow 1098)					nm: 2	2 20	
Figs. 17, 25B					sm: 4	4 4 2	
					st:	2	
<u>C. subdentata<sup>e</sup></u>	46	2.55 - 10.21	4	10 8 24	m: 4	10	14, SUBE
(Meerow 1156)					nm:	2 4 8	
Figs. 16, 25A					sm:	6 2 6	
					st:	2 2	

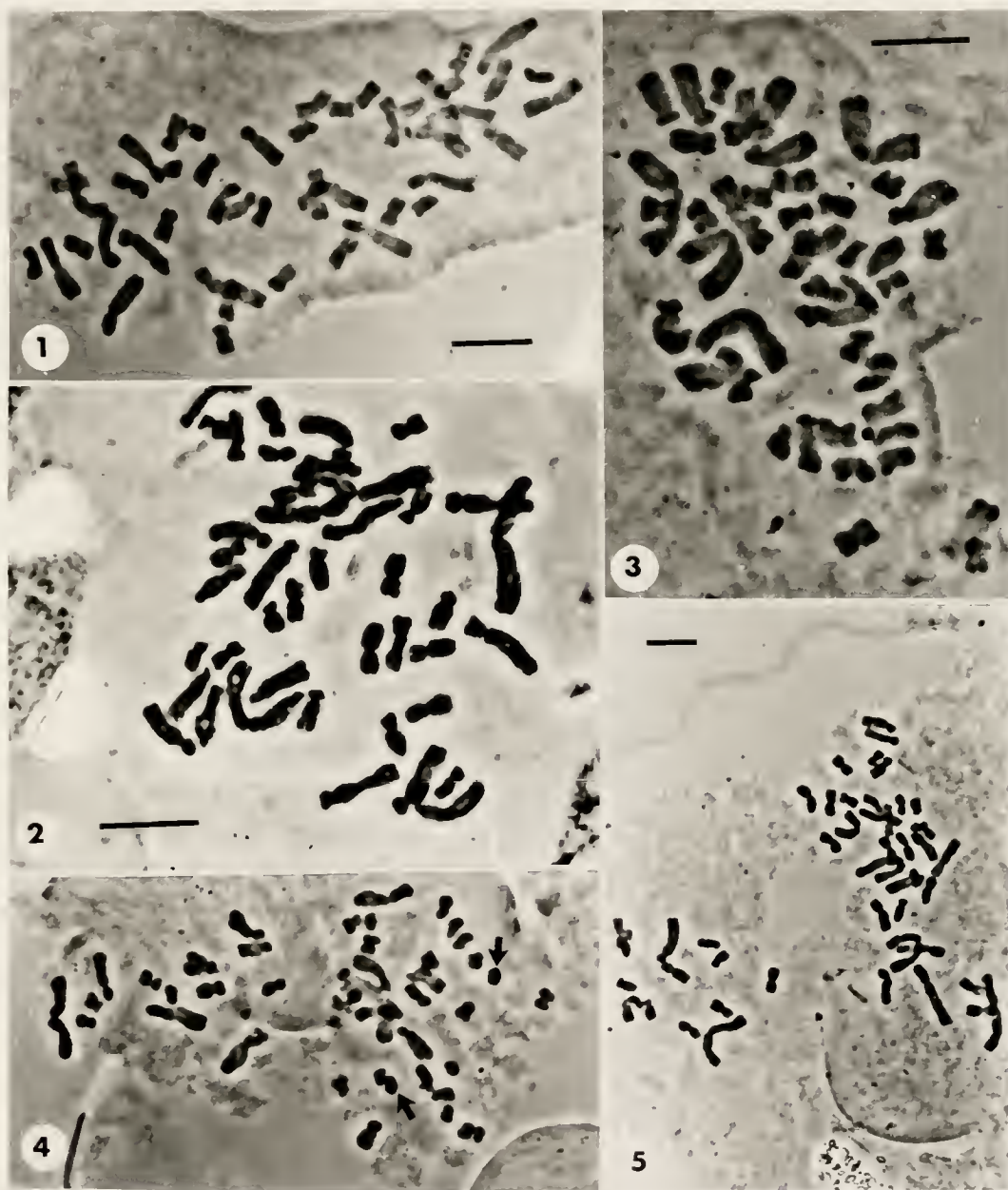




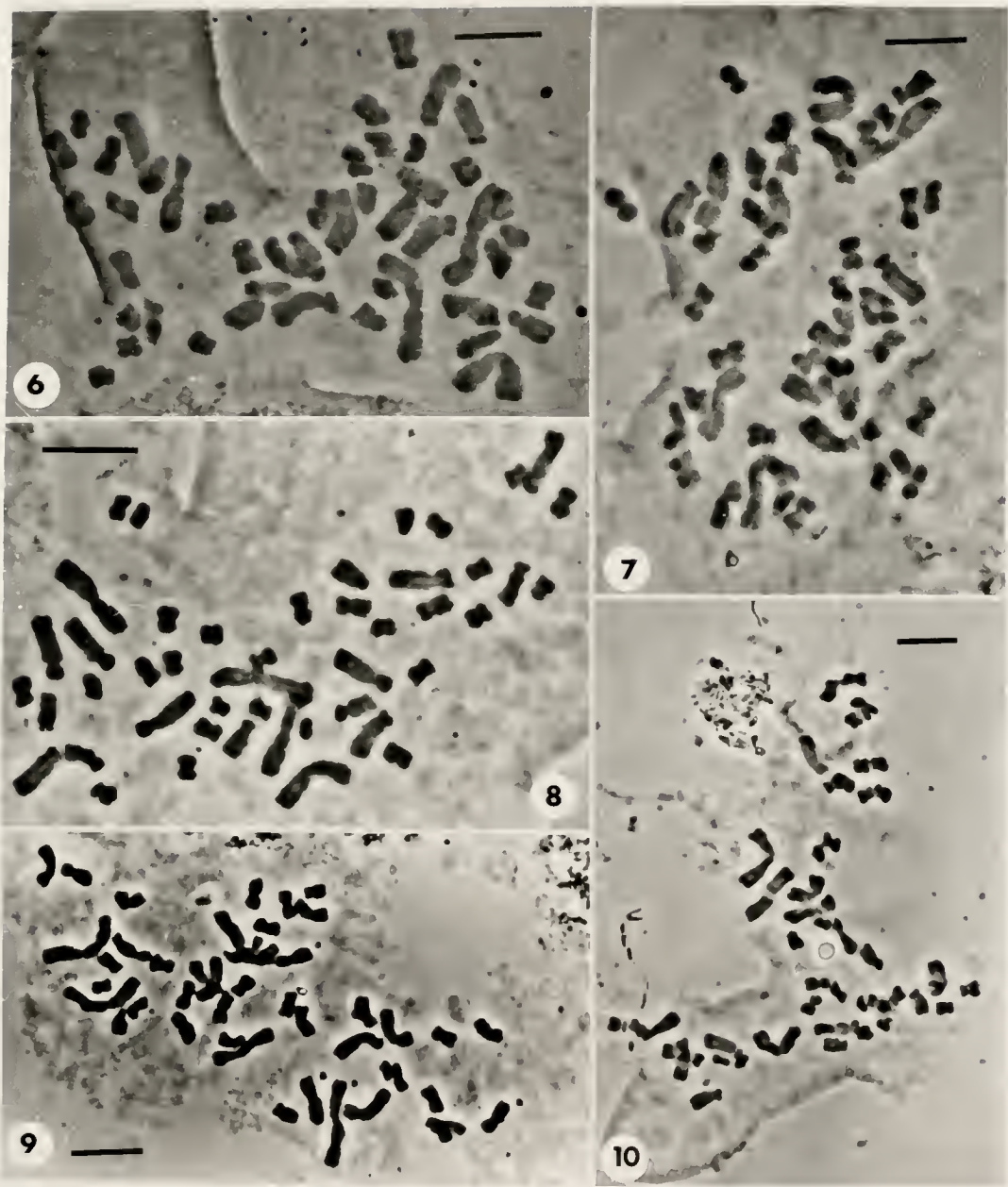
Table 7.2. First three principle components for multivariate analysis of karyotypes of Eucharis, Caliphruria, and Urceolina.

CHARACTER NUMBER	COMPONENT NUMBER		
	1	2	3
1	0.231	-0.062	0.172
2	0.369	0.207	0.189
3	0.232	0.440	-0.291
4	-0.101	-0.264	-0.416
5	-0.490	0.565	0.004
6	0.196	-0.006	-0.639
7	-0.058	0.240	-0.243
8	0.072	-0.014	-0.161
9	0.303	0.236	-0.187
10	0.125	-0.244	-0.302
11	0.169	-0.367	0.112
12	0.562	0.196	0.194
13	0.085	0.155	0.086

Figures 7.1-7.5. Root-tip cell mitotic metaphase configurations of Eucharis species. 1. E. astrophiala. 2. E. candida. 3. E. bakeriana. 4. E. castelnaeana. Arrows indicate telocentric chromosomes. 5. E. cyaneosperma. All scales = 10  $\mu$ m.

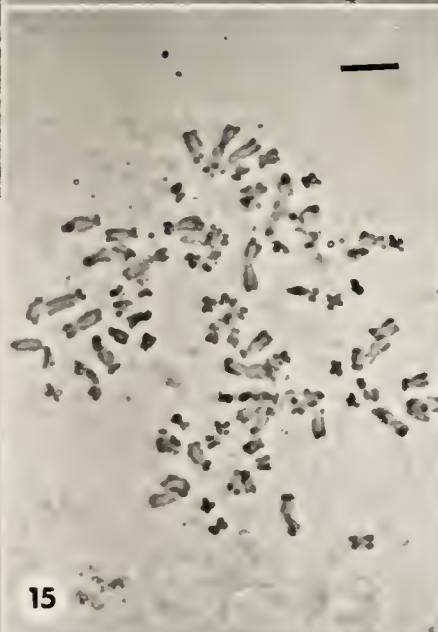
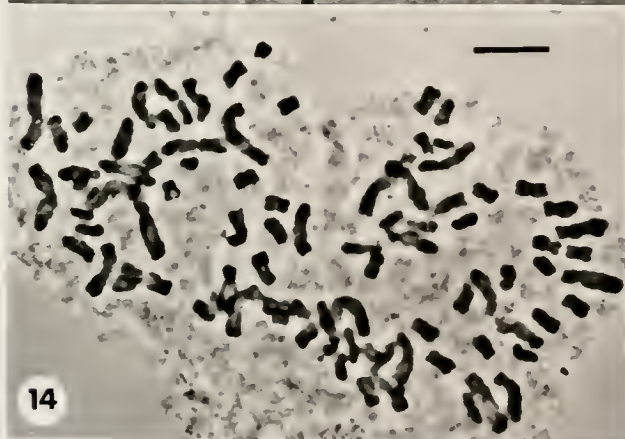
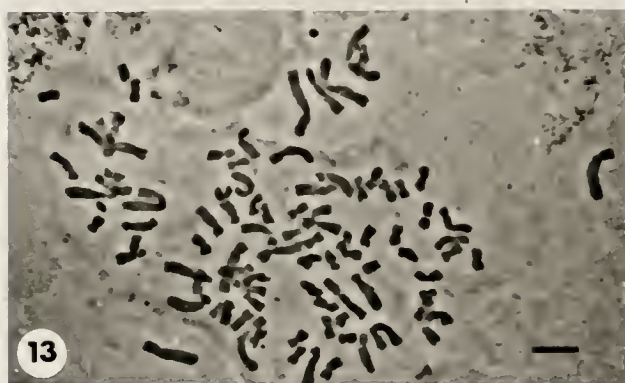
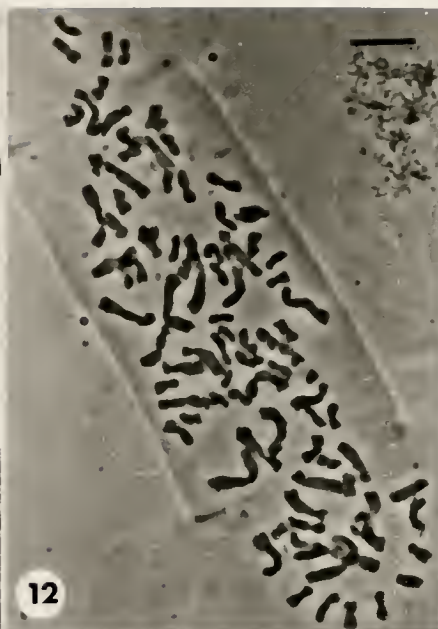
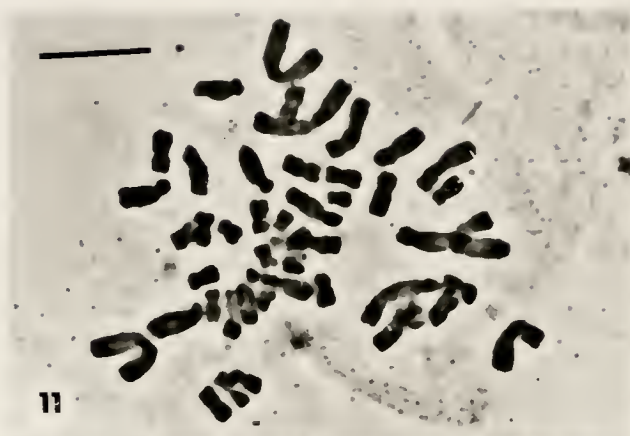


Figures 7.6-7.10. Root-tip cell mitotic metaphase configurations of Eucharis species. 6. E. formosa from Peru. 7. E. formosa from Ecuador. 8. E. plicata subsp. plicata. 9. E. ulei. 10. E. plicata subsp. brevidentata. All scales = 10  $\mu\text{m}$ .





Figures 7.11-7.15. Root-tip cell mitotic metaphase configurations of Eucharis species. 11-12. E. bouchei var. dressleri. 11. Diploid cell. 12. Tetraploid cell. 13. E. bouchei var. bouchei from Colón province in Panama. 14. E. bouchei var. bouchei from Coclé province in Panama. 15. E. bonplandii. Two small chromosomes are outside the figure frame. ATT scales = 10  $\mu$ m.



Figures 7.16-7.21. Root-tip cell mitotic metaphase configurations of Eucharis and Caliphruria species and hybrids. 16. C. subidentata. Arrows indicate heteromorphic homologs. 17. C. korsakoffii. 18. E. anomala. Arrows indicate telocentric chromosomes. 19. E. amazonica. 20. E. X grandiflora. 21. X Calicharis butcheri. All scales = 10  $\mu$ m.

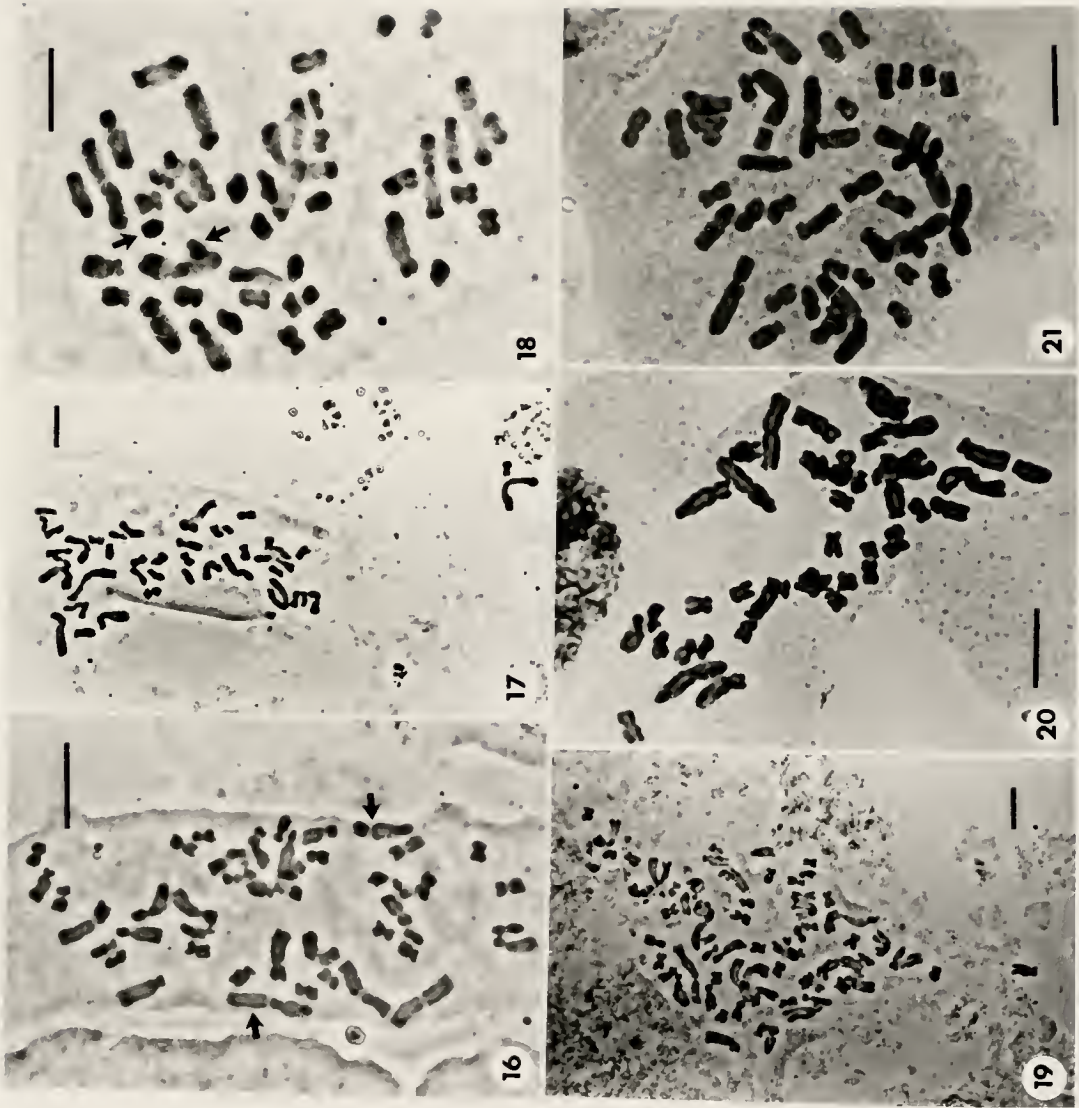
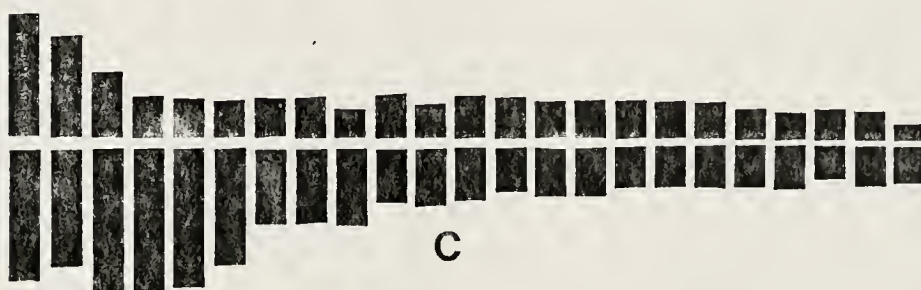
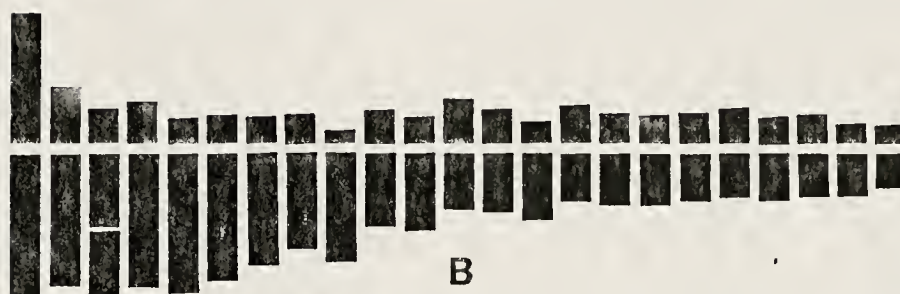
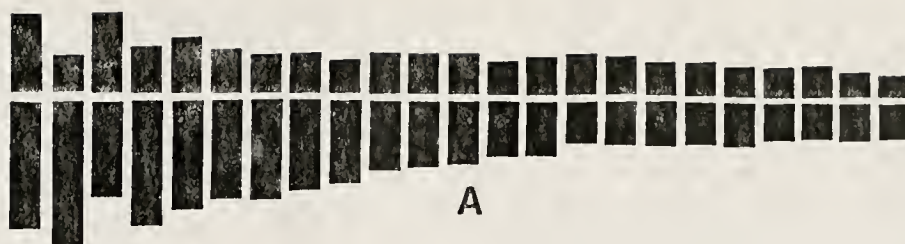


Figure 7.22. Haploid idiograms of Eucharis karyotypes. A. E.  
astrophiala. B. E. bakeriana. C. E. candida. D. E.  
castelnaeana. E. E. cynaenosperma.

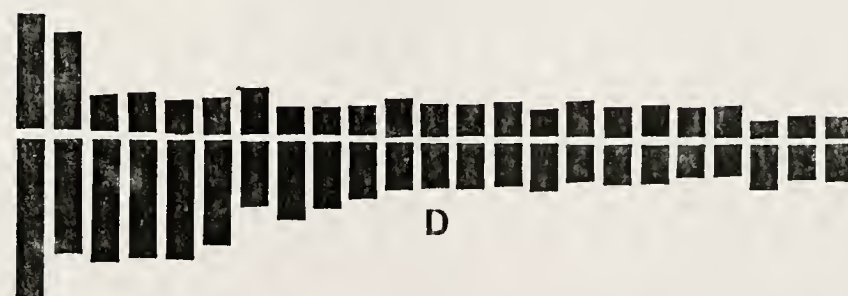
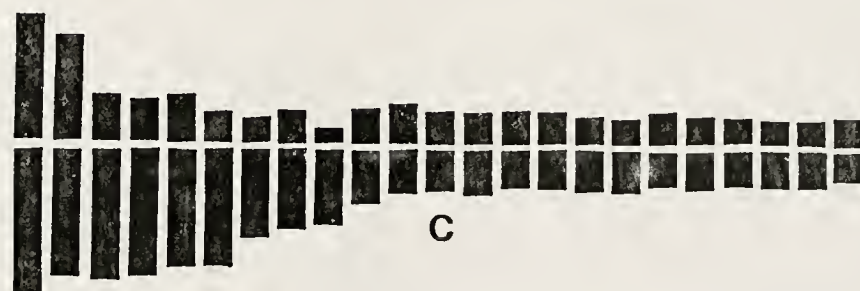
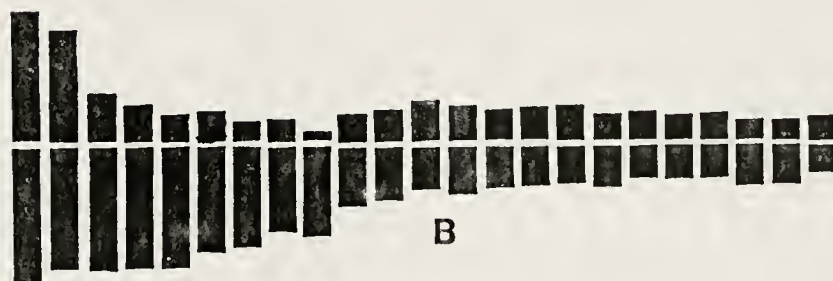
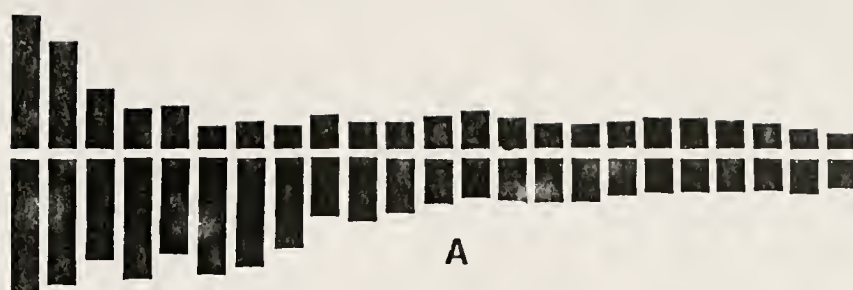




1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23

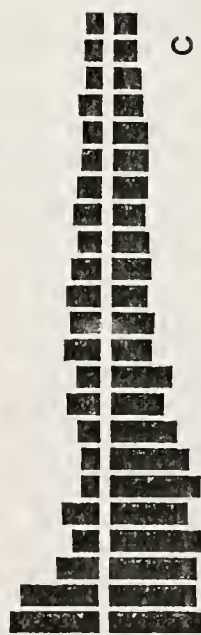
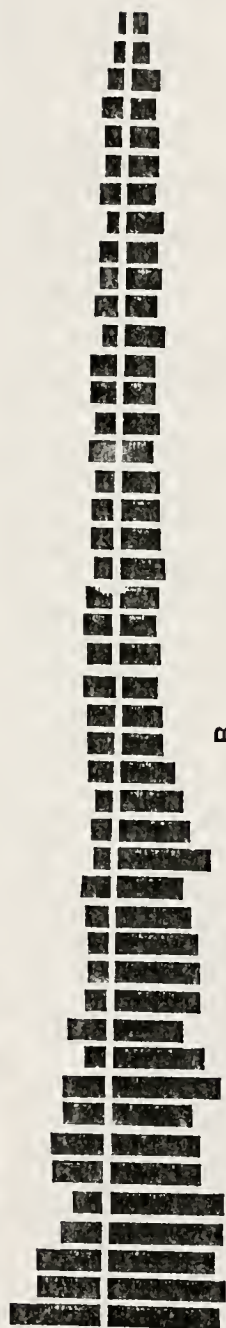
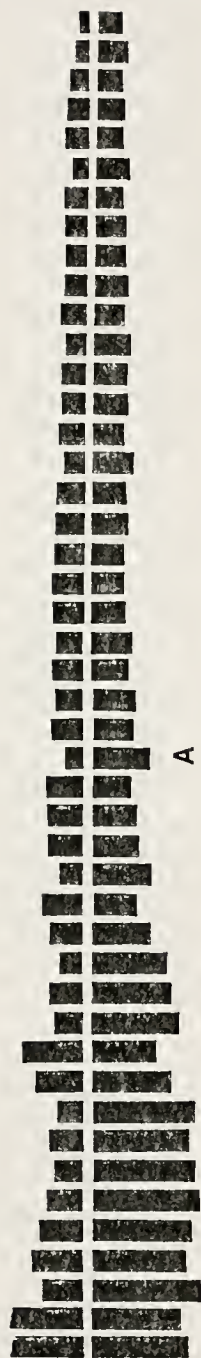


Figure 7.23. Haploid idiograms of Eucharis karyotypes. A. E. formosa from Peru. B. E. formosa from Ecuador. C. E. plicata subsp. plicata. D. E. plicata subsp. brevidentata. E. E. ulei.



1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23

Figure 7.24. Haploid idiograms of Eucharis karyotypes. A. E. bouchei var. bouchei from Colón province in Panama. B. E. bouchei var. bouchei from Coclé province in Panama. C. E. bouchei var. dressleri, diploid cell. D. E. bonplandii.



1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46

Figure 7.25. Haploid idiograms of Eucharis and Caliphruria karyotypes.

A. C. subdentata. Letters A and B indicate heteromorphic homologs. B. C. korsakoffii. C. E. anomala. D. E. amazonica.  
E. E. X grandiflora. E. X Calicharis butcheri.

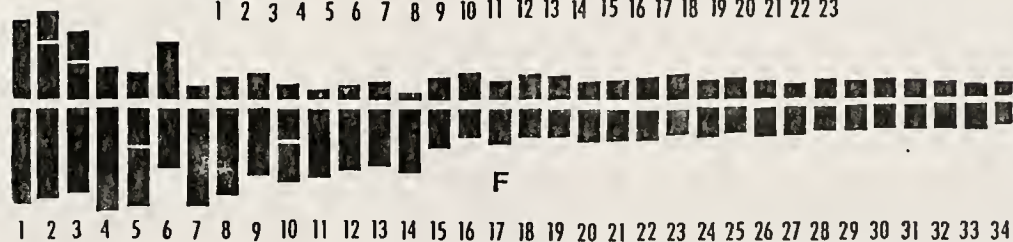
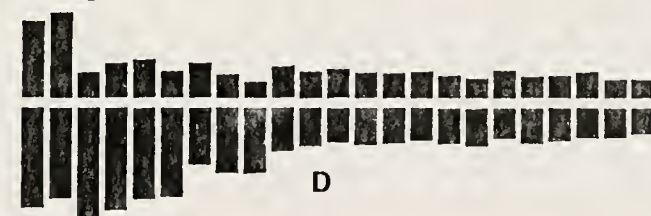
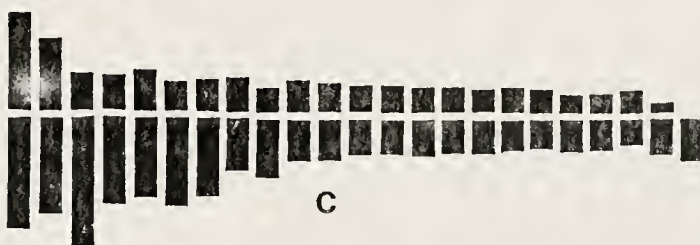
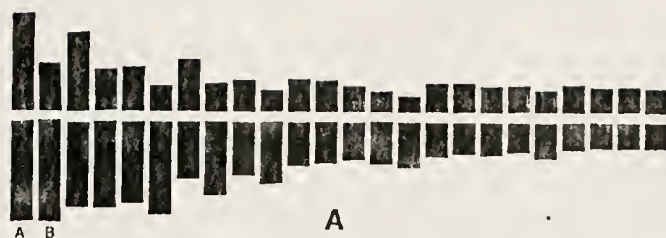




Figure 7.26. Root-tip cell mitotic metaphase configuration and haploid  
idiogram of Urceolina microcrater.



Figure 7.27. PCA scattergram of karyotype variance among fifteen Eucharis, Caliphruria, and Urceolina species. Refer to Table 1 for data matrix and OTU designations.

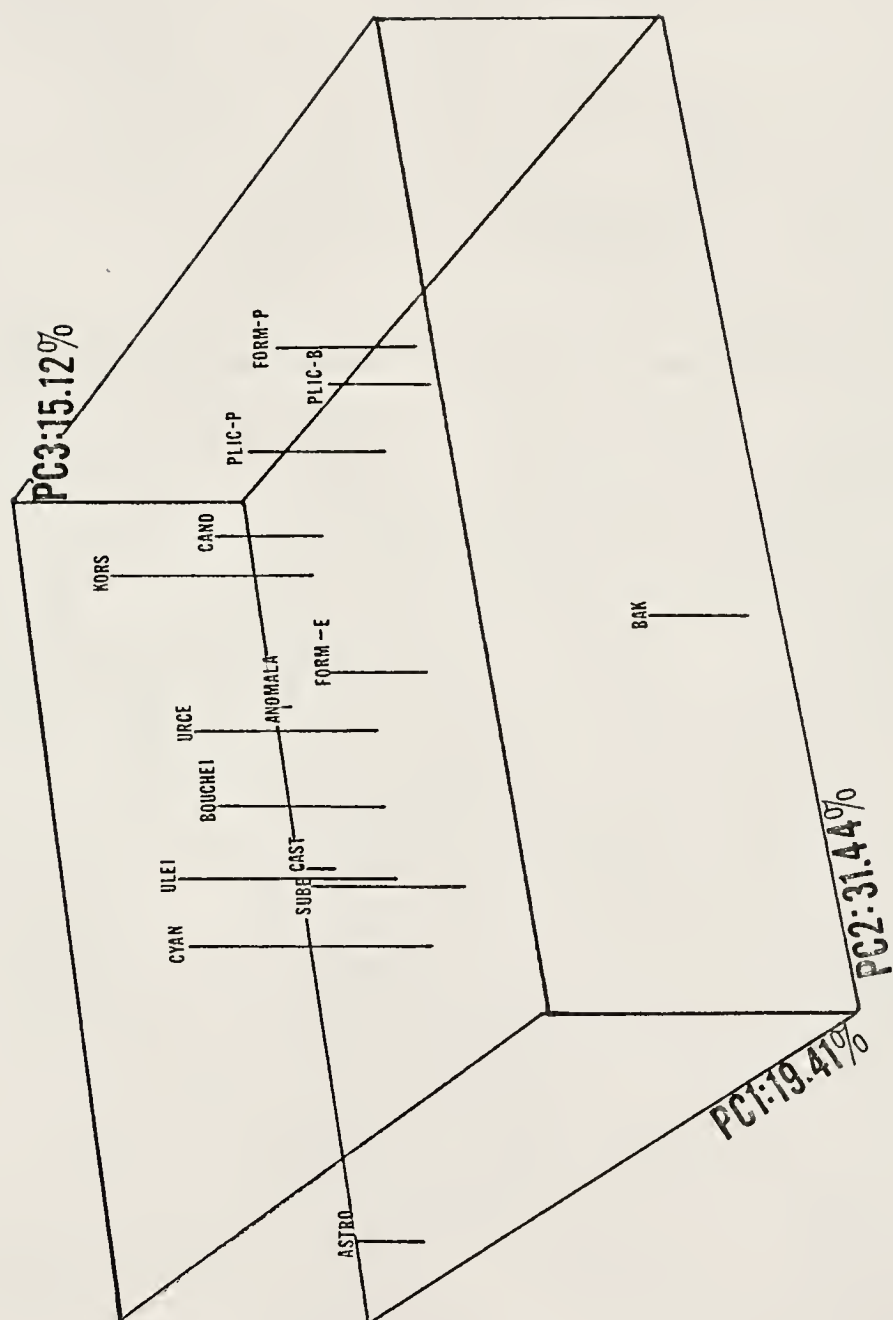
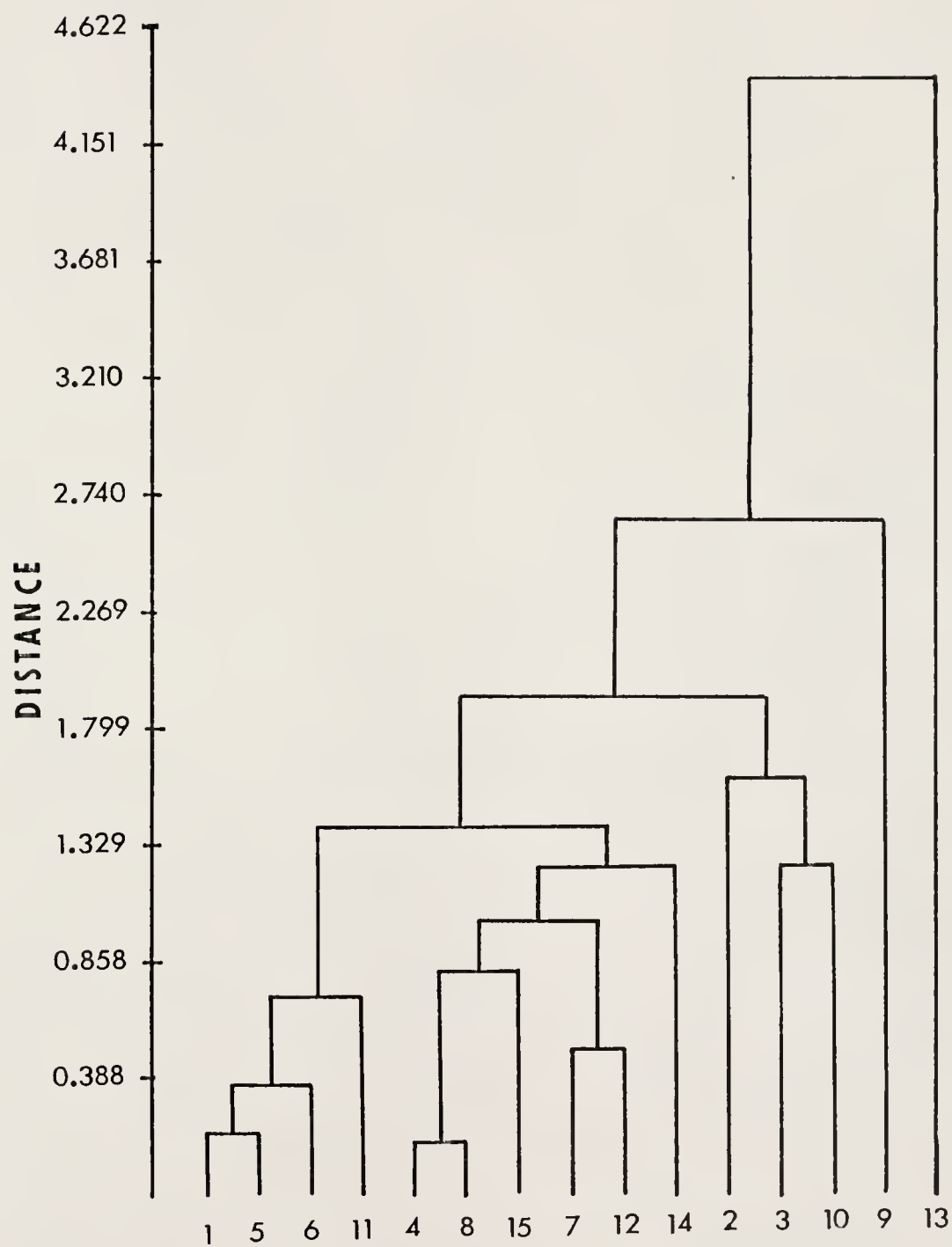


Figure 7.28. UPGMA dendrogram of karyotype variance among fifteen Eucharis, Caliphruria, and Urceolina species. Refer to Table 1 for data matrix and OTU designations.





## CHAPTER VIII

### ELECTROPHORETIC ANALYSES OF ISOZYME VARIATION

The use of electrophoretic analyses of isozyme variation in plant systematics has recently begun to be applied widely, and has been the subject of several reviews (Gottlieb, 1971, 1977, 1981a, 1982, 1984; Crawford, 1983, 1985). A number of investigations (e.g. Gray et al., 1973; Lee and Fairbrothers, 1973; Scogin, 1969), or reviews (Turner, 1969) of this application of electrophoresis concluded that isozyme variation in plants was too extensive to be successfully applied to systematic and phylogenetic questions. Unfortunately, most of these early, and even some more recent, studies (e.g., Payne and Fairbrothers, 1976) focused on non-specific enzyme systems such as esterases, peroxidases and phosphatases, which have large numbers of isozymic forms and thus generate complex electrophoretic phenotypes consisting of numerous bands (Gottlieb, 1977; Crawford, 1983). Interpretation of such complex banding patterns requires formal genetic analysis with a large population of segregating progeny (Crawford, 1983), as has been effectively demonstrated by Rick and coworkers (e.g., Rick et al., 1976, 1977; Rick and Tanksley, 1981) for Lycopersicon (Solanaceae).

Gel electrophoresis can be applied to a wide variety of phylogenetic and systematic problems which more traditional morphological criteria fail to resolve (Crawford, 1983; Gottlieb, 1977; Sytsma and Schaal, 1985). Unlike many morphological characters, which may demonstrate a great deal of environmental or developmental

plasticity, the electrophoretic phenotype is more directly equatable with genotype.

Electrophoretic evidence can be utilized to address: (1) genetic variation among conspecific populations (e.g., Crawford and Bayer, 1981; Crawford and Smith, 1984; Gottlieb, 1975; Soltis, 1981; see Crawford, 1983 and Gottlieb, 1977, 1981a for additional references); (2) genetic divergence among congeneric species, with attendant focus on the genetic processes of speciation (e.g., Crawford and Smith, 1982a, b; Gottlieb, 1973a, b; Heywood and Levin, 1984; Haulfler, 1985; Lowrey and Crawford, 1985; Soltis, 1985; Sytsma and Schaal, 1985; Werth et al., 1985; see Crawford, 1983, 1985 and Gottlieb 1977, 1981a for other references); (3) resolution of polyploid taxa and insight into their origins (e.g. Bayer and Crawford, 1986; Crawford and Smith, 1984; Gottlieb, 1973c, 1981b; Roose and Gottlieb, 1976; Soltis, 1986); (4) origins of cultivated plants (e.g., Decker, 1985; Doebley et al., 1984; Rick and Fobes, 1975a; Torres et al., 1978); and (5) testing hypotheses of broad systematic or evolutionary significance, e.g., genetic variation in relation to breeding system (Allard, 1975; Allard and Kahler, 1971), edaphic specialization (Babbel & Selander, 1974), interspecific (Levin, 1975) or intergeneric (Soltis and Soltis, 1986) hybridization.

A great deal of the recent work applying gel electrophoresis to problems in plant systematics has been conducted by Crawford or Gottlieb and their coworkers (see Crawford, 1983, 1985 and Gottlieb, 1977, 1981a, 1982 for extensive literature reviews). Much of this work has focused on annual or herbaceous perennial temperate zone plants in a few families, e.g., Asteraceae, Onagraceae, most of which occur in large populations. Electrophoretic studies of both woody and tropical plants

are not plentiful (Sytsma and Schaal, 1985). Plants with limited or rare distributions in the wild have also not been widely investigated. Malaysian Dipterocarpaceae have been subjects of limited isozyme studies (Gan et al., 1977; Gan et al., 1981; Ashton, et al., 1984). Genetic variation in South American Lycopersicon species has been studied in detail (Rick and Fobes, 1975a, 1975b; Rick et al., 1976, 1977). Hunziker and Schaal (1983) investigated isozyme variation in three species of Bulnesia, a woody genus of South American Zygophyllaceae. A phylogeny of Solanum sect. Lasiocarpa (Solanaceae) of northern South America, based heavily on isozyme data, was detailed by Whalen and Caruso (1983). Hawaiian species of Tetramolopium (Asteraceae) were surveyed for evidence of allozyme divergence (Lowrey and Crawford, 1985). Sytsma and Schaal (1985) studied genetic variation in the shrubby species of Lisianthus (Gentianaceae) in Panama.

Eucharis are exclusively tropical plants of rainforest understory. They are rare and widely dispersed in the wild, and are petaloid monocots. Studies of genetic variation of any plant group fitting just one of these three characteristics are very limited. Thus, an attempt to quantify isozyme variation in Eucharis, which fits all three conditions, seemed a worthy avenue of investigation.

### Materials and Methods

#### Population and Material Selection

Two complexes of populations were selected for analysis of isozyme variation: (1) the E. bouchei tetraploid complex of Panama, and (2) the

E. candida/formosa complex of Amazonian Ecuador, two phenetically distinct but often sympatric species.

Eucharis bouchei complex (Table 1, Fig.1). Eucharis bouchei is a tetraploid and highly polymorphic complex of Central American Eucharis. The species is concentrated in Panama, but collections have been made in Costa Rica and Guatemala. I recognize three varieties chiefly on the basis of staminal cup morphology (Chapter XII). Five populations were included in this analysis. These included three populations of E. bouchei var. bouchei, one from El Valle de Antón in Coclé province of Panama, and one each from Cerro Brujo and Río Iguanitas respectively in Colón province; and one population of var. dressleri, also from El Valle. The fifth population represented E. bonplandii, a rare species from Colombia, also tetraploid. These taxa are the only tetraploid species so far encountered in Eucharis. Sample size varied from population to population (Table 1) but did not exceed three plants in any one population.

Eucharis candida/formosa complex (Table 2, Fig. 2). Eucharis candida and E. formosa are the only species found in Amazonian Ecuador north of the Río Pastaza valley. From herbarium study alone, these species form a mosaic of flower size and staminal cup morphology that seemed taxonomically insoluble until living material was flowered in cultivation. They often grow sympatrically, and several putative hybrids have been collected. Both species occur in Amazonian Peru and Colombia as well, but are rarer outside of Ecuador. Four populations of E. formosa and two of E. candida were involved in the analysis. The fourth population of E. formosa represented a Peruvian population of the species. Two putative hybrid populations were also included in the

analysis. Sample size was one in all but the Limoncocha population of E. formosa, where  $n = 3$ .

A note on population number and sample size. In each of these studies, I have included as many populations of a particular taxon as were available (and assignable to species) in living plant collections. Crawford (1983) and Gottlieb (1977, 1981a) have surveyed genetic identities among conspecific plant populations. Genetic identities range from 0.87-1.00, with the greatest number above 0.95. Gottlieb (1981a) stressed plant breeding system as an important factor by which to regulate sample size for isozyme studies. Inbreeding plants either exhibit very little genetic variation among populations, or else wide variation due to large differences in allelic frequency (Crawford, 1983; Crawford and Wilson, 1977, 1979; Nevo et al., 1979). This uncertainty suggests that a greater number of populations should be sampled for autogamous species. Gottlieb (1981a) contends that one population of a particular species, especially if it is an outcrosser, provides most of the isozyme variation encountered in the species as a whole. The presence of interspecific and inter-subgeneric hybrids in nature, and evidence from greenhouse pollination and hybridization tests suggests that most Eucharis are out crossers (see Chapter X).

There is no particular consensus on the number of individual plants of each population to sample for electrophoretic analyses (Brown and Weir, 1983; Crawford, 1983; Gottlieb, 1977). Gottlieb (1977) suggests that the number of individuals to sample is best approached from the perspective of how many are required to have a 95% certainty of observing all the alleles at a locus which have frequencies greater than 0.05 each. Nei (1978) states that larger sample sizes are necessary



when the number of loci assayed is low, and may be appreciably smaller when numerous loci are analyzed. Much of the electrophoretic studies in plant systematics have involved taxa of characteristically large population size in nature. Populations of Eucharis, however, are characteristically small. The largest population I have encountered in the field (E. anomala) consisted of about fifteen individual clumps of bulbs in an approximate half-hectare area. Throughout eastern Ecuador, populations of only 2-3 genets (and frequently as low as one) of E. candida, E. formosa, and E. anomala are the norm. In eastern Peru, a careful search through a five hectare area turned up only two plants of E. cyaneosperma. Eucharis astrophiala, endemic to north- and central western Ecuador also frequently occurs as single, widely dispersed clumps. Herbarium specimens of Eucharis regularly include some notation indicating the rarity of the plants encountered. However, if Eucharis are primarily visited by trap-lining insects flying long distances, as I hypothesize (see Chapter X), population size from the perspective of potential gene exchange may in fact be greater than otherwise expected from known population densities.

#### Isozyme Extraction and Electrophoresis

Crude extracts for isozyme electrophoresis were prepared by grinding ten 1 mm diameter leaf discs in 1 ml of extraction buffer [100 mM Tris-HCl, 10 mM DTT, 20% glycerol, and 1 mM PMSF adjusted to pH 6.8 (Hames and Rickwood, 1981)]. Extracts were centrifuged twice, for 10 minutes and 2 minutes respectively, and the supernatant was decanted by pipette after each centrifugation.



Electrophoresis was performed on a BIO-RAD Protean II polyacrylamide gel apparatus. Gel recipes were adopted from Hames and Rickwood (1981). Running gels were 0.75 mm thick and 7.5% acrylamide (10 ml 30% acrylamide-bis acrylamide, 10 ml 1.5 tris-HCl at pH 8.8, 19.85 ml H<sub>2</sub>O, 100 µl 10% ammonium persulfate, and 15 µl TEMED). A 2.5% acrylamide stacking gel (1 ml 30% acrylamide-bis acrylamide, 1.92 ml 0.5 M tris-HCl at pH 6.8, 9 ml H<sub>2</sub>O, 20 µl ammonium persulfate, and 7.5 µl TEMED) was employed. Running buffer was 25 mM tris-glycine at pH 8.3 (Hames and Rickwood, 1981). A 20 µl sample of the supernatant was loaded into each stacking gel column. Gels were electrophoresed at a constant current of 50 mA until a blue indicator line (40 µl of bromophenol blue added to cathodal buffer) migrated off the anodal end of the gel, generally 4-5 hours.

Seven enzyme systems in total were assayed: alcohol dehydrogenase (ADH), aspartate dehydrogenase (AAT), glucose-6-phosphate dehydrogenase (G6PDH); glutathione reductase (GSSGR), malate dehydrogenase (MDH), phosphogluco-isomerase (PGI), and shikimate dehydrogenase (SKDH). Staining recipes of Vallejos (1983) were followed for ADH, AAT, G6PDH, PGI, and SKDH. All but AAT (diazonium system) utilize the tetrazolium system for staining activity. The tetrazolium system stain for MDH was that of Shaw and Prasad (1970). The tetrazolium system stain for GSSGR was that of Kaplan (1968).

Resolution of additional enzyme systems (galactose dehydrogenase, glutamate dehydrogenase, hexokinase, and isocitrate dehydrogenase) using the same buffer system were unsuccessful. Extracts of Eucharis leaf tissue are characteristically mucilaginous, which may impede electrophoretic separation or contribute to the degradation of some

enzymes after extraction. Also, cathodally migrating isozymes cannot be resolved in the same vertical, acrylamide gel as anodally migrating isozymes. Future work is planned with starch gels and alternative buffer systems.

### Inferring Genotypes

Without the benefits of electrophoretic phenotypes of segregating progeny, genotypes must be inferred directly from the electromorph patterns of the plants sampled. The perennial growth habit, annual flowering phenology, low seed yield of Eucharis fruits, plus the difficulty in flowering some species in cultivation, are obstacles to generating a substantial  $F_1$  population. Artificial hybridization of greenhouse collections of Eucharis has only recently been successfully accomplished, and will aid immeasurably in future electrophoretic studies.

Aiding in the problem of genotype inference were 1) the highly conserved nature of both enzyme substructure (Gottlieb, 1981c) and number and compartmentalization of loci coding for enzyme systems of high specificity (Gottlieb, 1982). Banding patterns observed in the populations presented herein were consistent with patterns observed in populations of other Eucharis species for which data are not presented. Where electromorphs were resolved in two well-separated regions of the gel (e.g., AAT), patterns within each region among polymorphic populations suggested that a single locus was represented at each region. In MDH, loci are not well-separated on the gels. This enzyme system characteristically yields complex phenotypes with formation of inter-locus heterodimers and, at times, overlap of isozymes (Kirkpatrick

et al., 1985; Torres, 1982). My interpretation of four discrete loci for MDH is drawn from patterns of polymorphisms observed in a number of other Eucharis species, and is consistent with reports of 3-4 isozymes of MDH for most diploid plants surveyed (Gottlieb, 1982).

Where several putative isozymes were observed, the most anodally migrating isozyme was numbered 1. Slower isozymes then were numbered successively towards the cathodal end of the gel. The most anodal allozyme was designated a, with slower forms successively assigned the labels b, c, etc.

### Data Analysis

Genotype data was analyzed using BIOSYS release 1 by David L. Swofford and Richard B. Selander (University of Illinois at Urbana-Champaign) on the NERDC computer system of the University of Florida.

A number of statistical coefficients have been devised to place allele frequency data into a single statistic of either genetic similarity or distance (Cavalli-Sforza and Edwards, 1967; Edwards, 1971, 1974; Hedrick, 1971; Nei, 1972, 1975, 1978; Rogers, 1972; Wright, 1978). Avise (1974) and Wright (1978) reviewed these measures in detail. All appear to provide similar estimates (Avise, 1974; Gottlieb, 1977). The genetic identity (I) and distance (D) coefficients of Nei (1972) are the most widely used statistical measure in the literature. Small sample size and low number of loci examined increases the bias of estimates of both average heterozygosity, and genetic distance (Nei, 1978). Nei (1978) presented modified formulae for unbiased genetic identities and distances that could be used for small sample size. Nei stressed that with a limited population sample, a large number of loci must be

analyzed. I have opted to use the unbiased D and I values for my analysis where sample size was greater than one. Nei (1972) values were used for all populations of a sample size of one. At all taxonomic levels within Eucharis, unbiased (Nei, 1978) values were closer than biased values (Nei, 1972) to average identities and distances reported for numerous genera of plants analyzed at the same taxonomic levels (see reviews of Gottlieb, 1977, 1981a, and Crawford, 1983). Nei also stated that the magnitude of sampling bias is less severe if genetic distances are high among the organisms under study ( $> 0.15$ ). Most of the values for D between the Eucharis populations assayed are well above 0.15. Mean heterozygosity, however, is high in Eucharis (generally over 0.15), which also can bias estimates of genetic identity and distance in cases of both small locus and small sample size (Nei, 1978). Consequently, the data on genetic variation presented below should be interpreted with caution until a larger number of either individuals within populations or loci are assayed. A larger data base will also allow statistically significant tests of conformation to Hardy-Weinberg equilibrium [e.g., the Fixation Index (Jain and Workman, 1967; Wright, 1969), which measures excess or deficiency of heterozygote proportions from Hardy-Weinberg estimations].

## Results

### Eucharis bouchei complex (Figs. 1, 3-4; Table 1, 3-5)

Enzyme systems assayed were AAT, MDH, GSSGR, PGI, and SKDH. Nine putative loci were inferred from the electrophoretic phenotypes, coded by 23 alleles (Table 3). Only SKDH was monomorphic across all

populations of E. bouchei and E. bonplandii. Only polymorphic loci are discussed below in detail and diagrammed in Fig. 3.

AAT (Figs. 3A, 4). Two well-separated isozymes were resolved for AAT, one rapidly migrating anodally (AAT-1) and the other (AAT-2) considerably slower. Electromorphs at both loci were considerably more complex than in diploid species of Eucharis. Three alleles were inferred from the phenotypes of AAT-1 in the E. bouchei complex. Each allele of AAT-1 in all Eucharis characteristically resolves as two, very closely spaced bands (Fig. 3). This is likely the result of breakdown products forming after extraction (Fig. 1 in Shields et al., 1983). Electromorphs of pollen of diploid Eucharis (Meerow, unpubl. data) also showed this banding pattern. Were each component band of the doublet a distinct allele, pollen would be expected to show only one of the two (Gottlieb, 1982, 1984).

Allele a was the most common allele of AAT-1, found in all individuals analyzed except for two homozygotes for allele c (the Cerro Brujo population and one individual of the El Valle population of var. bouchei). Variety dressleri and E. bonplandii are homozygous for allele a. The Río Iguanitas individual of var. bouchei is heterozygous for alleles a and b, while two individuals of the El Valle population have all three alleles.

Seven different alleles were inferred from phenotypes of AAT-2, and four E. bouchei individuals resolved a four-banded electromorph. Diploid species of Eucharis resolve only a one or two-banded electromorph for this isozyme. Alleles f and g were found only in E. bonplandii. Only two bands were observed in var. dressleri (an unstable tetraploid), representing alleles a and b or b and c, and one individual



of var. bouchei from El Valle (alleles c and d). All other individuals of E. bouchei resolved a four-banded electromorph for AAT-2. Allele e was found only in one individual of var. bouchei from El Valle. As all diploid species of Eucharis species resolve only a one- or two-banded electromorph for this isozyme, it was inferred that the proliferation of alleles within E. bouchei represented the additive effects of tetraploidy (Crawford, 1983, 1985; Gottlieb, 1982). In order to determine allele frequencies of these tetraploid phenotypes, putative geotypes had to be inferred in the absence of segregating progeny. I have opted to consider all alleles present in the tetraploid, heterozygous genotypes of AAT to be represented equally. No obvious dosage effects were visible in the electromorph patterns. Nonetheless, unequal representation of any one allele in these tetraploid genotypes remains a possibility. Alternative genotypes (e.g, aaab instead of abab) were analyzed with BIOSYS, and genetic identities did not fluctuate widely from the values reported below.

MDH (Figs. 3B, 4). Four loci were inferred from the phenotypes of MDH, coded by 8 alleles. MDH-2, MDH-3, and MDH-4 each resolved two alleles. Three or four isozymes of MDH are characteristically found plants (Gottlieb, 1982). MDH-1, the most anodal, is monomorphic in all populations of E. bouchei, but resolved two alleles and their heterodimer in E. bonplandii [pollen of this species resolved only a single band at this locus in a repetitive run (unpubl. data), supporting this interpretation]. MDH-2 is heterozygous across all populations. Dosage effects were apparent in homozygous phenotypes for allele a in MDH-3, and allele b in MDH-4 (Fig. 4). Eucharis bonplandii is heterozygous at all four loci.



PGI (Fig. 4). Only a single region of activity was resolved for PGI. Two alleles were observed, but allele a was found only in the heterozygotes (2 individuals of E. bouchei var. dressleri, and one of var. bouchei from El Valle).

GSSGR (Fig. 4). Two alleles were observed in the single locus resolved for GSSGR. No heterozygote phenotypes were found.

Genetic variation (Table 4). Percentage of polymorphic loci (P) ranges from 33.3-77.8%. Percentage of polymorphic loci in E. bouchei alone is 49.9%; for E. bonplandii P = 55.6%. Mean number of alleles per locus ( $\bar{k}$ ) ranges from 1.6-2.2. Mean heterozygosity per locus (H) across all populations ranges from 0.194-0.346. Average heterozygosity is 0.256 in populations of E. bouchei alone, and 0.278 in E. bonplandii. The El Valle population of E. bouchei var. bouchei in particular is extremely heterozygous (P = 78%,  $\bar{H}$  = 0.346). Gottlieb (1981a) reported average values for outcrossing species of  $\bar{P}$  = 33.3% and  $\bar{H}$  = 0.086 in a survey of isozyme variability of plant populations. Gottlieb's report is for diploid species, however. Increased heterozygosity is an expected consequence of allopolyploidy (Crawford, 1983, 1985; Gottlieb, 1981; Soltis and Rieseberg, 1986). A certain degree of fixed heterozygosity would also be expected in an allopolyploid (Gottlieb, 1981; Soltis and Rieseberg, 1986), due to the presence of two genomes in the allotetraploid. The heterozygous state for AAT-2 and MDH-2 is fixed across all four populations of Eucharis bouchei.

Genetic identities (Table 5) were lowest between all pairwise comparisons of E. bouchei populations and E. bonplandii (0.501-0.694,  $\bar{I}$  = 0.607). Genetic identity is also low (0.632-0.807,  $\bar{I}$  = 0.731) between E. bouchei var. dressleri and all populations of var. bouchei. Genetic

identity between the El Valle (Coclé province) and Río Iguanitas (Colón) populations of var. bouchei is high (0.951). These populations, while geographically separate, are similar in floral morphology. The Cerro Brujo population of var. bouchei (Colón province) shows a measure of genetic divergence from the the El Valle and Río Iguanitas populations with attendant lowered identity values (0.902 and 0.632 respectively). The very low value of I between the Río Iguanitas population and the Cerro Brujo population (0.632) is closer to the range usually found between congeneric species (Crawford, 1983, 1985; Gottlieb, 1977, 1981a). A sample size of one, however, for both the Río Iguanitas and Cerro Brujo populations undoubtedly make these values biased to some degree (Nei, 1978). Nonetheless, the phenetic heteromorphism of E. bouchei is paralleled in isozyme relationships as well. Mean infraspecific genetic identity among all populations of E. bouchei is only 0.784. Mean infravarietal genetic identity in E. bouchei var. bouchei is 0.836.

#### Eucharis candida/formosa complex (Figs. 2, 5-6; Table 2, 6-8)

Enzyme systems assayed were AAT, ADH, MDH, GSSGR, and SKDH. Eight putative loci coded by 18 alleles were inferred from the electrophoretic phenotypes (Table 6). Only ADH was monomorphic across all populations of the two species and putative hybrids. Only polymorphic loci are diagrammed in Fig. 6 and discussed below in detail.

AAT (Figs. 5A, 6). Two well-separated isozymes were resolved for AAT, one rapidly migrating anodally (AAT-1) and the other (AAT-2) considerably slower. Each of three alleles (a, b, and c) of AAT-1 resolved as a two-banded electromorph. This is likely the result of

breakdown products forming after extraction (see Fig. 1 in Shields et al., 1983). Three ab heterozygotes were observed, the Puyo population of E. candida, the Río Coca hybrid, and the Peruvian population of E. formosa. A single individual of the Limoncocha population of E. formosa was a bc heterozygote. All other individuals were homozygous for allele b.

Three alleles were inferred from the electromorphs of AAT-2. Allele b was the most common, found in the heterozygous state with either allele a (Limoncocha E. formosa, Río Coca E. candida, and the Lago Agrio hybrid) or c (all other individuals).

MDH. (Figs. 5B, 6). Three loci coded by six alleles were inferred from the phenotypes. A fourth cathodal locus was apparent, but could not be adequately resolved. MDH-1, the most anodal isozyme, was also the most polymorphic, with three alleles observed. Allele c was the most common, represented in all populations. Homozygotes for allele c are all populations of E. formosa, and the putative hybrid from Río Coca. Allele b was the rarest allele, observed only in the heterozygous E. candida from Puyo (genotype bc). The putative hybrid from Lago Agrio, and E. candida from Río Coca are heterozygotes with the genotype ac, with heterodimerization between c and the rare allele a.

Two alleles were observed for MDH-2, a and b. The most common allele is b. Heterozygotes are both hybrids, the Tena population of E. formosa, and the Puyo population of E. candida. Only two homozygotes for a were observed, two individuals of E. formosa from Limoncocha.

Two alleles were also resolved for MDH-3. Allele b is found in only two individuals, homozygous E. candida from Puyo, and heterozygous E. formosa from Tena. All other populations were homozygous for a.

GSSGR (Fig. 6). Only a single anodal locus was successfully resolved for this enzyme. Two alleles were observed. Allele b is present only in the two heterozygotes, both E. candida, from Puyo and Río Coca respectively.

SKDH (Fig. 6). All populations except Peruvian E. formosa were homozygous for this monomorphic enzyme.

Genetic variation (Table 7). Percentage of polymorphic loci (P) ranges from 12.5-62.5%. For E. candida  $P = 50\%$ , and in E. formosa, 31.3%. Mean number of alleles per locus ( $\bar{k}$ ) ranges from 1.1-1.6. Mean heterozygosity per locus (H) across all populations ranges from 0.063-0.313. Average heterozygosity for populations of E. candida is 0.260, and 0.148 for E. formosa. These values of H are high in comparison to Gottlieb's (1981a) reported average for outcrossing, diploid species (0.086), especially the average value of E. candida, but P for E. formosa agrees closely with his value (33.3%). The Eucharis populations are also depauperate in mean number of alleles per locus based on Gottlieb's (1981a) averages. Heterozygosity at the AAT-2 locus appears fixed across all populations analyzed. The Pastaza population of E. formosa is homozygous at all loci except AAT-2. Heterozygosity estimates of these Eucharis populations are, however, biased to an uncertain degree by the small sample size (Nei, 1978).

Mean genetic identity (Table 8) among all pairwise combinations of E. formosa populations is 0.900. Among only Ecuadorean populations of E. formosa,  $\bar{I} = 0.927$ . Identity between the two E. candida populations is very low, 0.669. Average identity between E. candida and E. formosa is 0.788. The Puyo population of E. candida has the lowest range of genetic identities with all populations analyzed (0.669-0.836), and

shows lower genetic identity with the single other conspecific population (0.669) than with the Tena population of E. formosa (0.836). The individual representing E. formosa from Pastaza has high genetic identities with all populations of either species (0.895-0.931), except E. candida from Puyo (0.701). The putative hybrids generally have values of genetic identity intermediate between those of both species ( $I = 0.885$ ), but both have very high  $I$  values with the Limoncocha population of E. formosa (0.946, 0.972). These values are higher than any between the Ecuadorean populations of E. formosa (0.917-0.934)

### Discussion

Studies of isozyme variation in plants allow several generalizations to be made concerning degrees of genetic divergence at various taxonomic levels (Gottlieb (1977, 1981a; Crawford, 1983). Mean genetic identities among conspecific plant populations of diverse taxa from widely unrelated families range from 0.87-1.00, with the greatest percentage above 0.95. At this level of the taxonomic hierarchy, autogamous species usually show higher values than out-crossing species (Gottlieb, 1981a). Genetic similarity among subspecific taxa is generally the same as for conspecific populations of the same taxon (Crawford, 1983, 1985). By contrast, genetic identities among congeneric species are much lower (Crawford, 1983, 1985; Gottlieb, 1977, 1981a), with a mean value ca 0.67. In these contexts, values of Nei (1972, 1978) genetic identities and distances among populations of two species complexes of Eucharis, one diploid, the other tetraploid, offer insight into their relationships.



### Eucharis bouchei complex

Cluster analysis of the tetraploid Eucharis populations by the unweighted pair group method (UPGMA, Sneath and Sokal, 1973) using values of Nei (1972, 1978) genetic distance, graphically illustrates the isozyme relationships among these taxa (Fig. 7). The Cerro Brujo (Colón province) population of var. bouchei shows greater isozyme divergence from El Valle populations than does var. dressleri, also from El Valle. The Cerro Brujo population also exhibits karyotype divergence from the El Valle population (Chapter VII). Though floral morphological differences exist between the El Valle and Cerro Brujo populations of E. bouchei var. bouchei (Fig. 11 in Chapter XII), they are not discontinuous enough to warrant a clearcut differentiation of a fourth variety in the species. Furthermore, at least one Colón population (Río Iguanitas) has a high value of genetic identity (0.951) with the El Valle population. Divergence between the Coclé populations and those in Colón province (of which the Cerro Brujo population is one), presumably mediated by geographic isolation, may thus be an actively ongoing process.

Eucharis bouchei var. dressleri occurs sympatrically as a rare morph with populations of var. bouchei. This variety is an unstable tetraploid (see Chapter VII). Fifteen percent of all chromosome counts of root tip cell mitotic metaphase configurations have  $2n = 46$ , the typical diploid chromosome number in Eucharis. Variety dressleri lacks the additive banding patterns observed in both loci of AAT in all other populations of E. bouchei, a factor, perhaps, of this karyotypic instability. Additive enzyme banding patterns have been observed in a



number of tetraploid taxa of Gossypium (Cherry et al., 1972), Nicotiana (Reddy and Garber, 1971; Sheen, 1972; Smith et al., 1970), Triticum aestivum (Hart, 1970, 1979; Jaaska, 1978; Torres and Hart, 1976), and Stephanomeria (Gottlieb, 1973c), and are usually interpreted as indicative of allopolyploid origins (Crawford, 1983; Gottlieb, 1983; Soltis and Rieseberg, 1986). Pollen stainability of var. dressleri is 100% with Alexander's (1969) stain, suggesting that gamete formation is not impaired by the chromosome number instability. Nonetheless, I have not successfully crossed this variety with El Valle populations of var. bouchei.

The rare Colombian tetraploid, E. bonplandii, also lacks additive banding patterns for AAT. This may indicate an autopolyploid origin for this species (Crawford, 1985; Soltis and Rieseberg, 1986). Yet mean heterozygosity for this species is still high (0.278). Even if E. bonplandii is an autotetraploid, it has established a degree of genomic "hybridity" (Barber, 1970; Stebbins, 1980; Tal, 1980). Diploid species of Eucharis appear to be highly heterozygous themselves (see discussion of the E. candida/formosa complex). Consequently, an autotetraploid may have a degree of "advanced" heterozygosity built into its genome.

Isozyme analyses of polyploid taxa are not abundant (Crawford, 1985; Soltis and Rieseberg, 1986). There are no estimates of expected genetic identities among related polyploid taxa, in contrast to the data available for diploid taxa. Mean genetic identity among all populations of E. bouchei (0.784) is lower than the values usually reported for subspecific taxa and conspecific populations (0.90-1.00). This reflects the relatively high degree of heterozygosity in E. bouchei (Table 4),

which is itself good evidence for an allopolyploid origin of the species.

Genetic identity patterns similar to those found between the populations of var. bouchei (Table 5) were reported by Wain (1982) for three subspecies of the diploid Helianthus debilis (Asteraceae). Mean genetic identities among populations of each of the three subspecies were high (ca 0.99). Pairwise comparisons between populations of subsp. vestitus and tardiflorus yielded the same mean identity. When subsp. vestitus and tardiflorus were compared to populations of subsp. debilis [considered the most morphologically distinct of the three subspecies by Heiser (1956)], mean identities dropped to 0.886 and 0.902 respectively. Wain (1982) hypothesized a recent divergence of subsp. vestitus and tardiflorus from an ancestral population. Crawford (1985), reviewing the same data along with concordant data on two additional subspecies of H. debilis (Wain, 1983) suggested instead that subsp. debilis has been isolated geographically for a longer period of time than any of the other subspecies.

On the basis of staminal cup morphology I hypothesize that Eucharis bouchei has been steadily migrating away from the Colombian border (see Chapter IX and XII). The Cerro Brujo population of E. bouchei var. bouchei may fit Crawfords's (1985) model of H. debilis subsp. debilis. The Cerro Brujo population may represent an intermediate point in the divergence of a new geographical race of E. bouchei. The best test of this hypothesis would be the results of isozyme analysis of E. bouchei var. darienensis, the one variety for which material is not presently available. Variety darienensis is found closer to the Colombian border than any other population of E. bouchei, and has the most generalized

staminal cup morphology relative to Eucharis as a whole. If my hypothesis is correct, var. darienensis should have the lowest genetic identity with populations of either var. bouchei or var. dressleri from Coclé province, and higher identity with populations of var. bouchei from Colón province.

However, the Río Iguanitas and Cerro Brujo populations of var. bouchei, both from Colón province, have a particularly low value of genetic identity (0.656) between them. Colón populations of E. bouchei are geographically intermediate between most populations of var. darienensis and the Coclé populations of var. bouchei (see Fig. 12, Chapter XII). The two varieties come into close proximity in the Cerro Campana area in Panama province. Colón populations may therefore also be genetically intermediate between the two varieties. Segregating genotypes in such a case could produce populations exhibiting a mosaic of varying genetic identity, some close to Coclé var. bouchei, others perhaps closer to var. darienensis. Further testing of this hypothesis with var. darienensis and larger numbers of populations and individuals is necessary. The origin of E. bouchei var. dressleri, however, may be the first step in sympatric speciation. This variety shows highest genetic identity with the Coclé population of var. bouchei (0.807).

Average genetic identity between E. bonplandii and E. bouchei (0.607) is not far below the expected values for congeneric species (Crawford, 1983; Gottlieb, 1981a). The question of whether these two species represent a monophyletic group on the basis of their tetraploid origin is not conclusive. Eucharis bonplandii does not show any additive banding pattern at either locus of AAT, suggesting that its genomic constitution may be autopolyploid. The fact that E. bonplandii is

the northernmost species of Eucharis subg. Eucharis in South America, and is also tetraploid, lends at least circumstantial credence to the hypothesis that both E. bouchei and E. bonplandii represent divergences from a common tetraploid ancestor. The rare occurrence of polyploidy in Eucharis strengthens this possibility as well. The difficulty in obtaining successful meiotic figures from bulbs of Eucharis (microsporogenesis occurs completely inside the bulb) blocks the resolution of this question.

There is insufficient information on the breeding system and pollination biology of Eucharis to support more than ad hoc hypotheses of most species' origins. The characteristically small population sizes that are encountered throughout the range of the genus, may indicate that founder effects (Mayr, 1954; Templeton, 1980a, b) have played an important role in the movement of E. bouchei across the Isthmus of Panama, with subsequent isolation restricting gene flow between localized populations. The putatively allotetraploid genotype of E. bouchei would favor the "hybrid recombination" type of "genetic transilience," a mode of speciation hypothesized by Templeton (1980a, b). This is consistent with the low genetic identities between some populations of E. bouchei, all of which are geographically isolated (see Chapter XII). Additional support are the morphological novelties expressed within each geographical variety (or race, in the case of var. bouchei). Reduction in heterozygosity does not necessarily follow founder effects (Nei et al., 1975; Templeton, 1980a, b), but loss of alleles often does occur. Eucharis bouchei is highly heterozygous (Table 4), but most populations are somewhat depauperate in mean number of alleles per locus (Table 4) in comparison with out-crossing North

American species (Gottlieb, 1981a). Sytsma and Schaal (1985) reported similar findings and conclusions from isozyme analysis of the tetraploid Lisianthus skinneri (Gentianaceae) complex from Panama.

#### Eucharis candida/formosa complex

Cluster analysis of the E. candida/formosa complex by the unweighted pair group method [UPGMA (Sneath and Sokal, 1973)] using values of Nei (1972, 1978) genetic distance, graphically illustrates the isozyme relationships among these taxa (Fig. 8). Lower genetic identities between all pairwise combinations of E. formosa and E. candida ( $I = 0.785$ ) than among populations of E. formosa alone (0.900), suggest that these morphological species have diverged genetically to some extent. This between-species average value of identity, however, is higher than usually characteristic of outcrossing plants (Gottlieb, 1981a). The degree of divergence of the Puyo population of E. candida from all populations of either species is most striking. There is no obvious phenetic corroboration of this level of genetic divergence, and chromosome morphology of this population has not been examined. This population is also extremely heterozygous ( $H = 0.313$ ). Highest value of  $I$  (0.836) for this population is with the Tena population of E. formosa, the population of either species to which Puyo E. candida is geographically closest (Fig. 2).

The putative hybrids cluster with populations of E. formosa, the parent which they most resemble morphologically. Their average genetic identity (0.885) is intermediate between  $I$  of E. formosa (0.900) and E. candida (0.669), but their close genetic relationship to E. formosa occludes the hypothesis of hybridization between E. formosa and E.



candida suggested by phenetic analysis (Chapter VI). The Lago Agrio hybrid in particular, which phenetically is much closer to E. formosa, and whose pollen stains 100%, exhibits highest values of identity with Ecuadorean E. formosa (0.885-0.972). I suggest (Chapter XII) that this collection in fact may be a genet at the low-size end for E. formosa, and not a hybrid.

The chromosomal divergence of Peruvian E. formosa (Chapter VII) is reflected genetically as well. Genetic identities between Peruvian and Ecuadorian E. formosa range from 0.844-0.931, in contrast to a range of 0.917-0.934 among only Ecuadorean populations. Although Peruvian E. formosa does not obviously differ morphologically from Ecuadorean populations of the species, it appears that both chromosomal and isozymic divergence, mediated by geographical isolation, can precede phenetic divergence in Eucharis.

The nearly homozygous E. formosa from the Pastaza valley has high genetic identities with populations of both E. formosa and E. candida. Of all populations, it also has the highest identity with Peruvian E. formosa (0.931) of any Ecuadorean population. The Pastaza valley may therefore be the site of origin for both species, from which they have radiated, perhaps more than once. Cladistic analysis supports a progenitor-descendent relationship for these two species, and isozyme data suggest that species level genetic divergence has not yet advanced beyond the level usually characteristic of subspecific taxa. Further isozyme analyses of populations of both of these sympatric species may indicate a greater mosaic of genetic identity values than presently reported.



The relationship of E. candida and E. formosa is complicated by the likely prospect that both have been cultivated for many years by the native people of eastern Ecuador (see Chapter XII). Present-day populations may therefore not be "natural" populations, but rather remnants of shifting cultivation over long periods of time. A long history of cultivation of these two sibling species throughout the Amazon basin of Ecuador may have artificially reinforced gene flow between them, by continuously breaking down geographic barriers, and via natural hybridization within mixed, cultivated populations. The Puyo population of E. candida, with its large genetic distance from all other populations, may have remained isolated enough to escape this pattern.

There is an alternative explanation for the patterns of isozyme variation found in this complex. Successive fragmentation and expansion (with secondary contact) of ancestral panmictic populations, as is now largely accepted as having occurred in the Amazon basin during the Pleistocene (see Prance, 1983 for extensive review), could also have preserved genetic similarities between these two closely related species. The disparate genetic identities of the two E. candida populations with all other populations, and their low pair-wise identity, may even suggest that E. candida is polyphyletic. A larger number of populations of both species, but particularly E. candida, need to be analyzed electrophoretically before a firm answer is given.

Crawford (1983) offers three hypotheses to explain taxonomically difficult groups in which species boundaries are blurred morphologically, and presents expected values of genetic identity in each case: 1) taxa have originated recently and divergence is not yet appreciable (high genetic identities); 2) phenotypic plasticity is high

enough that divergent genomes converge phenotypically under similar conditions (low genetic identities); and 3) interspecific hybridization occurs between some populations of each species (low genetic identities between true species populations; "intermediate" values among the hybrids, and between them and true species). In the case of the E. candida/formosa complex, all three processes may be at work.

### Conclusions

Isozyme analysis of two species complexes of Eucharis indicates that the genus is still actively evolving. The Central American E. bouchei complex is a tetraploid, putatively allopolyploid, semi-species complex of morphologically distinct entities that shows low genetic identities between some geographically isolated populations. Founder effects and geographic isolation probably were, and still are, important forces influencing the continued evolution of E. bouchei. In one case (E. bouchei var. dressleri) sympatric divergence seems to be in process.

The E. candida/formosa group shows a more complex pattern of isozyme variation. Eucharis formosa, the more ancestral species cladistically, shows high genetic identities between populations. A Peruvian isolate of E. formosa, though not morphologically distinct, shows both chromosomal and isozymic divergence from Ecuadorean populations. Eucharis candida, the more derived species, appears genetically diverse on the basis of the limited populations surveyed. Hybridization and gene flow between both species has apparently occurred, mediated either by artificial population structures due to a probable long history of cultivation, or via Pleistocene refugia effects. Both

species may have originated in the Pastaza valley from a common ancestral population which has since radiated north and south, perhaps several times.

The high level of heterozygosity exhibited by Eucharis species, both diploid and tetraploid, raises an interesting question concerning ploidy level of the pancratioid Amaryllidaceae as a whole. Paleotropical genera of "infrafamily" Pancratioidinae characteristically have  $2n = 22$  or 20 chromosomes, while almost all neotropical genera have  $2n = 46$ . The latter number is likely derived through fragmentation or duplication of a single chromosome, followed by doubling of the genome (Lakshmi, 1978; Sato, 1938). Increased heterozygosity may therefore have accompanied a tetraploid origin of the neotropical tribes of the Pancratioidinae from an ancestor with  $2n = 22$ . The high generic diversity of neotropical pancratioids (ca 15 genera) in comparison to the paleotropical taxa (4 genera) may itself be partially a consequence of greater genetic variability. Comparative analysis of isozyme phenotypes between paleotropical and neotropical genera is planned, and may provide insight into the evolution of the Pancratioidinae.

Table 8.1. Eucharis bouchei and E. bonplandii populations examined electrophoretically

TAXON	DESIGNATION	COLLECTION INFORMATION	VOUCHER <sup>a</sup>
<u>Eucharis bouchei</u> <u>var. dressleri</u>	EBD	Panama, Coclé, El Valle de Antón	<u>Meerow 1107</u>
<u>E. bouchei</u> var. <u>bouchei</u>	EBB-1	Panama, Coclé, El Valle de Antón	<u>Meerow 1125</u>
<u>E. bouchei</u> var. <u>bouchei</u>	EBB-2	Panama, Colón, Río Guanche, Cerro Brujo	<u>Meerow 1157</u>
<u>E. bouchei</u> var. <u>bouchei</u>	EBB-3	Panama, Colón, Río Iguanitas	<u>Meerow 1158</u>
<u>E. bonplandii</u>	EBN	Colombia, Cundinamarca, vicinity of Bogotá	<u>Baum] 720 (HUNT)</u>

<sup>a</sup>All vouchers deposited at FLAS unless otherwise indicated.

Table 8.2. Eucharis candida, E. formosa and hybrid populations examined electrophoretically.

TAXON	DESIGNATION	COLLECTION INFORMATION	VOUCHER <sup>a</sup>
<u>Eucharis formosa</u>	EF-1	Ecuador, Napo, Limoncocha	Meerow 1103
<u>E. formosa</u>	EF-2	Ecuador, Napo, vic. Tena	Besse et al. s. n. (SEL)
<u>E. formosa</u>	EF-3	Peru, San Martin, Lamas	Schunke 14174
<u>E. formosa</u>	EF-4	Ecuador, Pastaza, Diez de Agosto	Meerow & Meerow 1131
<u>E. candida</u>	EC-1	Ecuador, Napo, Río Coca	Besse et al. s. n. (SEL)
<u>E. candida</u>	EC-2	Ecuador, Pastaza, Puyo	Meerow 1159
<u>E. candida</u> X <u>formosa</u>	EX-1	Ecuador, Napo, Río Coca	Besse et al. 1949 (SEL)
<u>E. candida</u> X <u>formosa</u>	EX-2	Ecuador, Napo, Lago Agrio	Besse et al. 1558 (SEL)

<sup>a</sup>All vouchers deposited at FLAS unless otherwise indicated.

Table 8.3. Allele frequencies in populations of Eucharis bouchei and E. bonplandii (N = sample size).

LOCUS AND ALLELES	POPULATION				
	EBD	EBB-1	EBB-2	EBB-3	EBN
N	3	3	1	1	1
AAT-1					
a	1.000	0.167	0.000	0.500	1.000
b	0.000	0.167	0.000	0.500	0.000
c	0.000	0.667	1.000	0.000	0.000
AAT-2					
a	0.167	0.083	0.250	0.250	0.000
b	0.500	0.167	0.250	0.250	0.000
c	0.333	0.333	0.250	0.250	0.000
d	0.000	0.333	0.250	0.250	0.000
e	0.000	0.083	0.000	0.000	0.000
f	0.000	0.000	0.000	0.000	0.500
g	0.000	0.000	0.000	0.000	0.500
MDH-1					
a	0.000	0.000	0.000	0.000	0.500
b	1.000	1.000	1.000	1.000	0.500
MDH-2					
a	0.500	0.500	0.500	0.500	0.500
b	0.500	0.500	0.500	0.500	0.500
MDH-3					
a	0.500	0.833	0.500	1.000	0.500
b	0.500	0.167	0.500	0.000	0.500
MDH-4					
a	1.000	0.167	0.500	0.000	0.500
b	0.000	0.833	0.500	1.000	0.500
SDH					
a	1.000	1.000	1.000	1.000	1.000
GSSGR					
a	0.000	0.333	1.000	0.000	1.000
b	1.000	0.667	0.000	1.000	0.000



Table 8.3--continued.

LOCUS AND ALLELES	POPULATION				
	EBD	EBB-1	EBB-2	EBB-3	EBN
FREQUENCIES					
N	2	2	1	1	1
PGI					
a	0.500	0.250	0.000	0.000	1.000
b	0.500	0.750	1.000	1.000	0.000

Table 8.4. Genetic variability measures across all loci in populations of Eucharis bouchei and E. bonplandii. n = sample size, k = mean number of alleles per locus, P = percentage of polymorphic loci, H = mean heterozygosity (standard errors in parentheses).

POPULATION	n	$\bar{k}$	p <sup>a</sup>	H
EBD	3.0	1.6 (0.2)	44.4	0.235 (0.093)
EBB-1	3.0	2.2 (0.4)	77.8	0.346 (0.080)
EBB-2	1.0	1.7 (0.3)	44.4	0.250 (0.102)
EBB-3	1.0	1.6 (0.3)	33.3	0.194 (0.100)
EBN	1.0	1.6 (0.2)	55.6	0.278 (0.088)

<sup>a</sup>A locus is considered polymorphic if the more than one allele was detected.

Table 8.5. Matrix of genetic identity and distance coefficients between populations of *Eucharis bouchei* and *E. bonplandii*. Below diagonal: Nei (1972, 1978) genetic identity; above diagonal: Nei (1972, 1978) genetic distance.

POPULATION	EBD	EBB-1	EBB-2	EBB-3	EBN
EBD	*****	0.214	0.459	0.283	0.365
EBB-1	0.807	*****	0.103	0.050	0.445
EBB-2	0.632	0.902	*****	0.422	0.523
EBB-3	0.754	0.951	0.656	*****	0.691
EBN	0.694	0.641	0.593	0.501	*****

Table 8.6. Allele frequencies in populations of Eucharis candida, E. formosa and hybrids (N = sample size).

LOCUS AND ALLELES	POPULATION							
	EF-1	EF-2	EF-3	EF-4	EC-1	EC-2	EX-1	EX-2
FREQUENCIES								
N	3	1	1	1	1	1	1	1
AAT-1								
a	0.000	0.000	0.500	0.000	0.000	0.500	0.500	0.000
b	0.833	1.000	0.500	1.000	1.000	0.500	0.500	1.000
c	0.167	0.000	0.000	0.000	0.000	0.000	0.000	0.000
AAT-2								
a	0.500	0.000	0.000	0.000	0.500	0.000	0.000	0.500
b	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500
c	0.000	0.500	0.500	0.500	0.000	0.500	0.500	0.000
MDH-1								
a	0.000	0.000	0.000	0.000	0.500	0.000	0.000	0.500
b	0.000	0.000	0.000	0.000	0.000	0.500	0.000	0.000
c	1.000	1.000	1.000	1.000	0.500	0.500	1.000	0.500
MDH-2								
a	0.667	0.500	0.000	0.000	0.000	0.500	0.500	0.500
b	0.333	0.500	1.000	1.000	1.000	0.500	0.500	0.500

Table 8.6--continued.

LOCUS AND ALLELES	POPULATION						
	EF-1	EF-2	EF-3	EF-4	EC-1	EC-2	EX-1 EX-2
FREQUENCIES							
MDH-3							
a	1.000	0.500	1.000	1.000	1.000	0.000	1.000
b	0.000	0.500	0.000	0.000	0.000	1.000	0.000
ADH							
a	1.000	1.000	1.000	1.000	1.000	1.000	1.000
SDH							
a	1.000	1.000	0.500	1.000	1.000	1.000	1.000
b	0.000	0.000	0.500	0.000	0.000	0.000	0.000
GSSGR							
a	1.000	1.000	1.000	1.000	0.500	0.500	1.000
b	0.000	0.000	0.000	0.000	0.500	0.500	0.000

Table 8.7. Genetic variability measures across all loci in populations of *Eucharis candida*, *E. formosa* and hybrids. n = sample size,  $\bar{k}$  = mean number of alleles per locus, P = percentage of polymorphic loci, H = mean heterozygosity (standard errors in parentheses).

POPULATION	n	$\bar{k}$	P <sup>a</sup>	H
EF-1	3.0	1.4 (0.2)	37.5	0.153 (0.078)
EF-2	1.0	1.4 (0.2)	37.5	0.188 (0.091)
EF-3	1.0	1.4 (0.2)	37.5	0.188 (0.091)
EF-4	1.0	1.1 (0.1)	0.0	0.063 (0.063)
EC-1	1.0	1.4 (0.2)	37.5	0.188 (0.091)
EC-2	1.0	1.6 (0.2)	62.5	0.313 (0.091)
EX-1	1.0	1.4 (0.2)	37.5	0.188 (0.091)
EX-2	1.0	1.4 (0.2)	37.5	0.188 (0.091)

<sup>a</sup>A locus is considered polymorphic if more than one allele was detected.



Table 8.8. Matrix of genetic identity and distance coefficients between population of *Eucharis candida*, *E. formosa* and hybrids. Below diagonal: Nei (1972, 1978) genetic identity; above diagonal: Nei (1972, 1978) genetic distance.

POPULATION	EF-1	EF-2	EF-3	EF-4	EC-1	EC-2	EX-1	EX-2
EF-1	*****	0.069	0.170	0.087	0.140	0.364	0.055	0.029
EF-2	0.934	*****	0.167	0.072	0.214	0.179	0.080	0.123
EF-3	0.844	0.846	*****	0.072	0.214	0.402	0.080	0.214
EF-4	0.917	0.931	0.931	*****	0.111	0.356	0.072	0.111
EC-1	0.870	0.808	0.808	0.895	*****	0.402	0.214	0.080
EC-2	0.695	0.836	0.669	0.701	0.669	*****	0.284	0.402
EX-1	0.946	0.923	0.923	0.931	0.808	0.753	*****	0.123
EX-2	0.972	0.885	0.808	0.895	0.923	0.669	0.885	*****

Figure 8.1. Distribution of Eucharis bouchei (Panama) and E. bonplandii (Colombia, inset) populations analyzed electrophoretically. Refer to Table 1 for population designations.

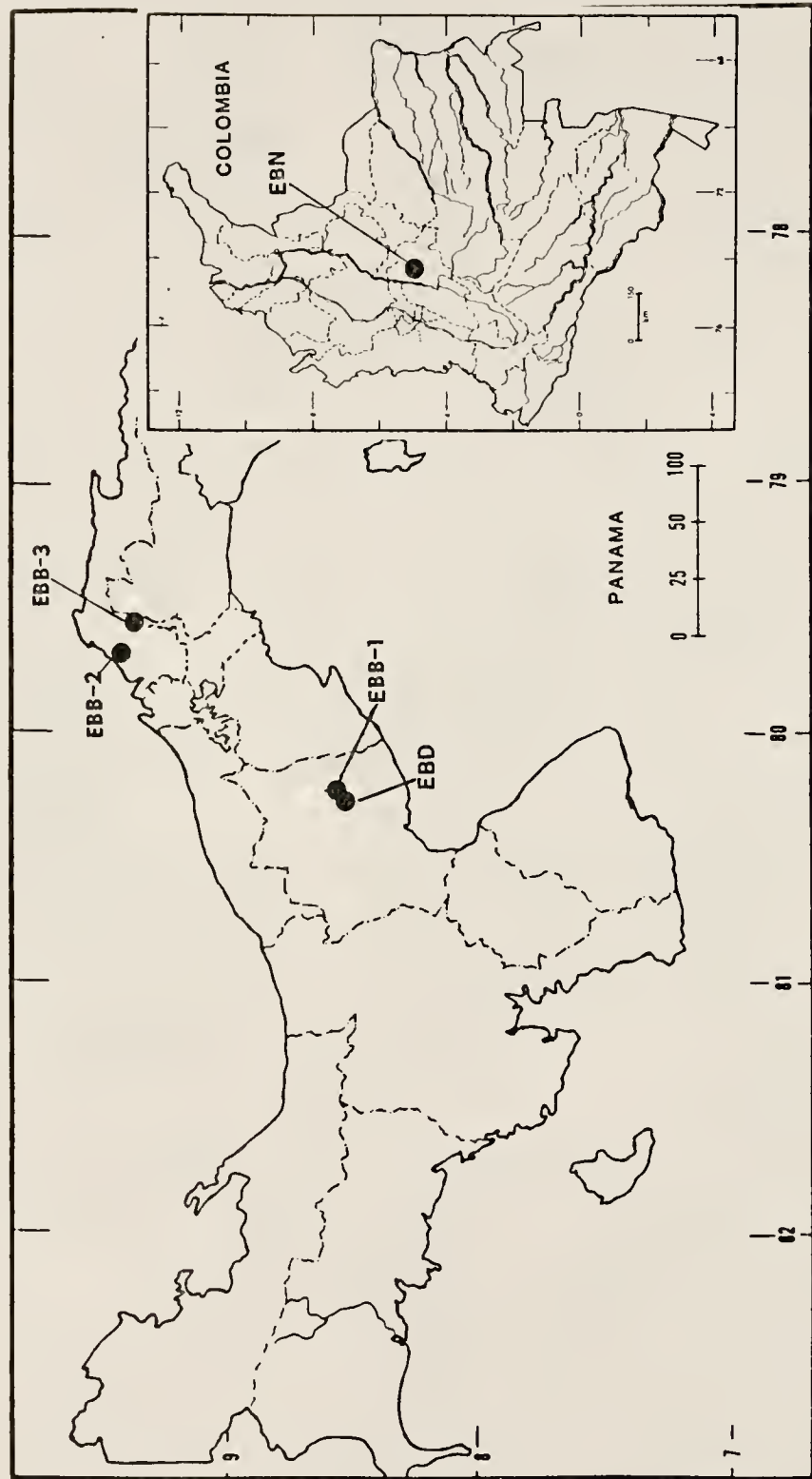


Figure 8.2. Distribution in Ecuador and Peru (inset) of Eucharis  
candida, E. formosa, and hybrid populations analyzed  
electrophoretically. Refer to Table 2 for population  
designations.

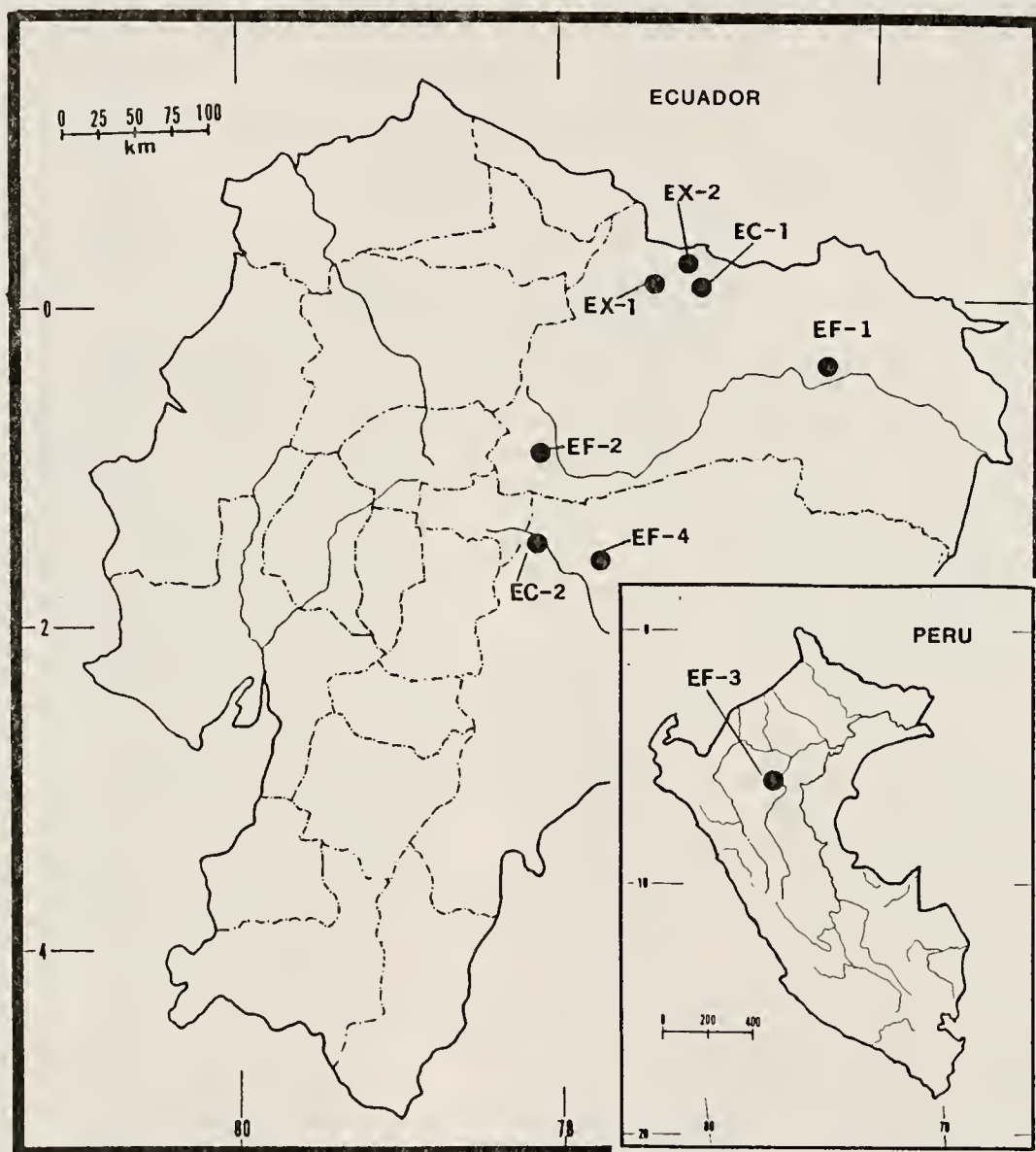


Figure 8.3. Representative gels for electrophoretic analysis of Eucharis bouchei complex. A. Aspartate amino transferase (AAT). B. Malate dehydrogenase (MDH). Where no activity is apparent, it was subsequently resolved in repetitive runs. Numbers and lower case letters to right refer to loci and alleles respectively. Refer to Table 1 for population designations.



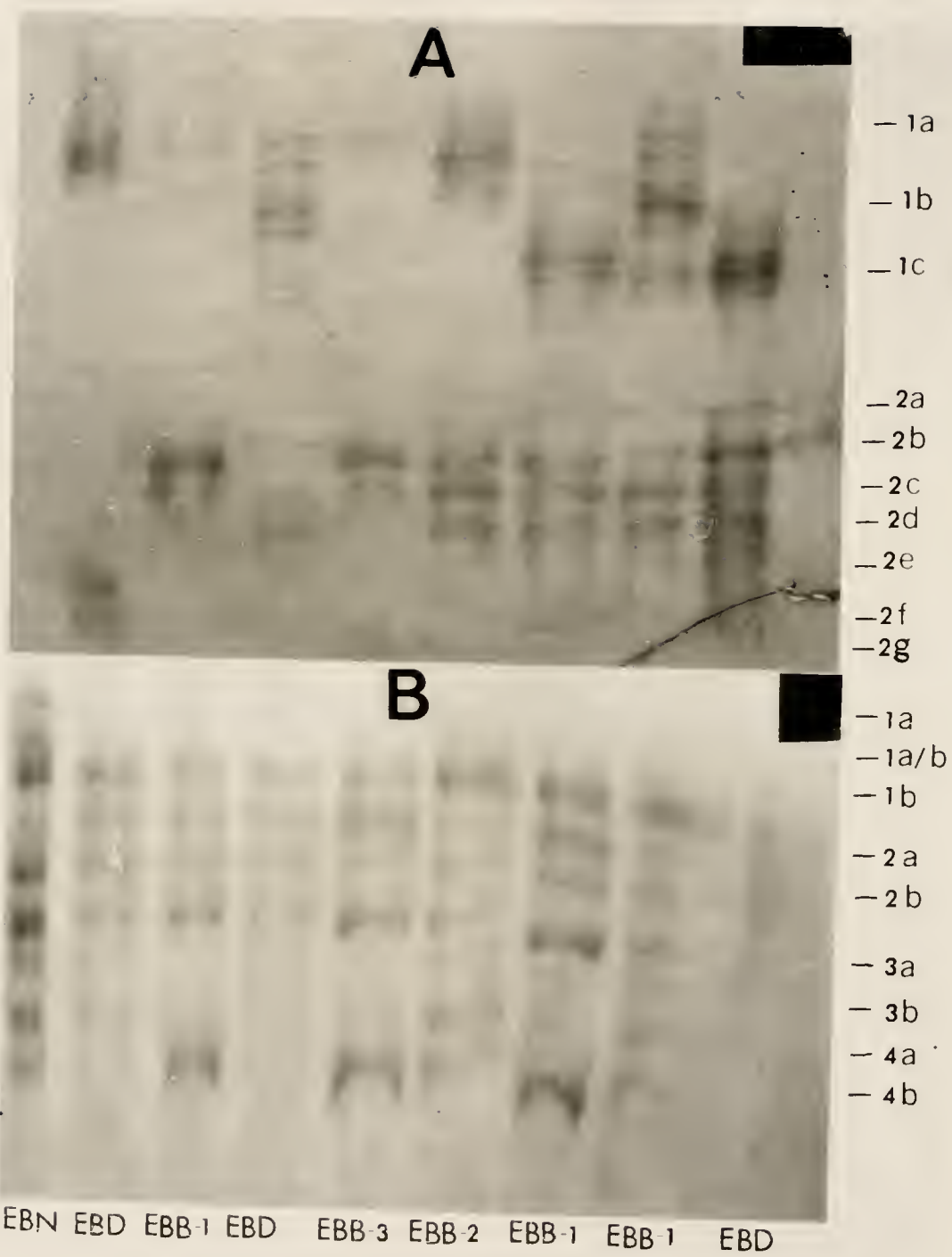


Figure 8.4. Electrophoretic phenotypes at all polymorphic loci in the Eucharis bouchei complex. Numbers and lower case letters to right refer to loci and alleles respectively. Refer to Table 1 for population designations. AAT = aspartate amino transferase, MDH = malate dehydrogenase, GSSGR = glutathione reductase, PGI = 6-P-glucose isomerase.

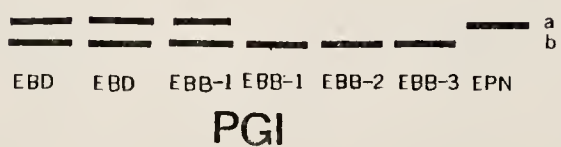
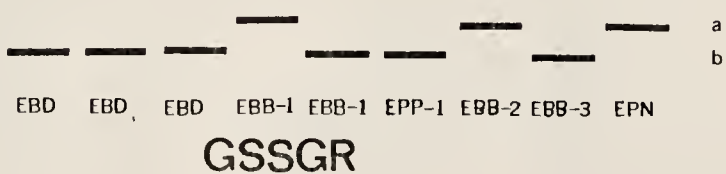
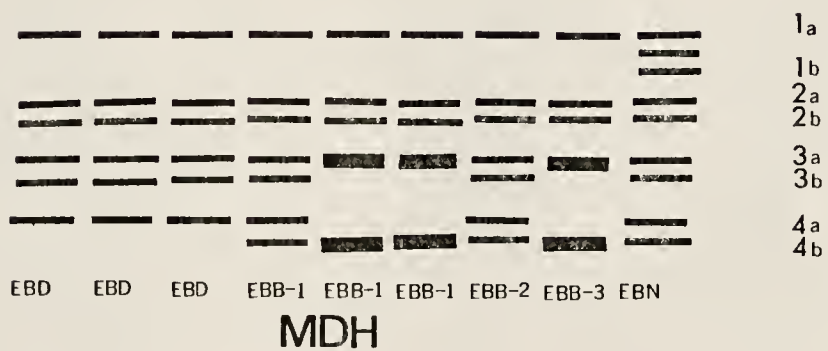
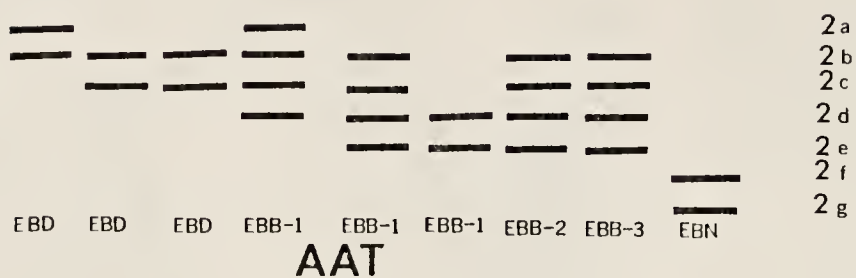
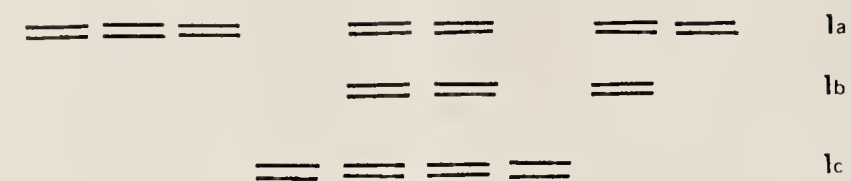


Figure 8.5. Representative gels for electrophoretic analysis of Eucharis candida/formosa complex. A. Aspartate amino transferase (AAT). B. Malate dehydrogenase (MDH). Where no activity is apparent, it was subsequently resolved in repetitive runs. Numbers and lower case letters to right refer to loci and alleles respectively. Refer to Table 2 for population designations.

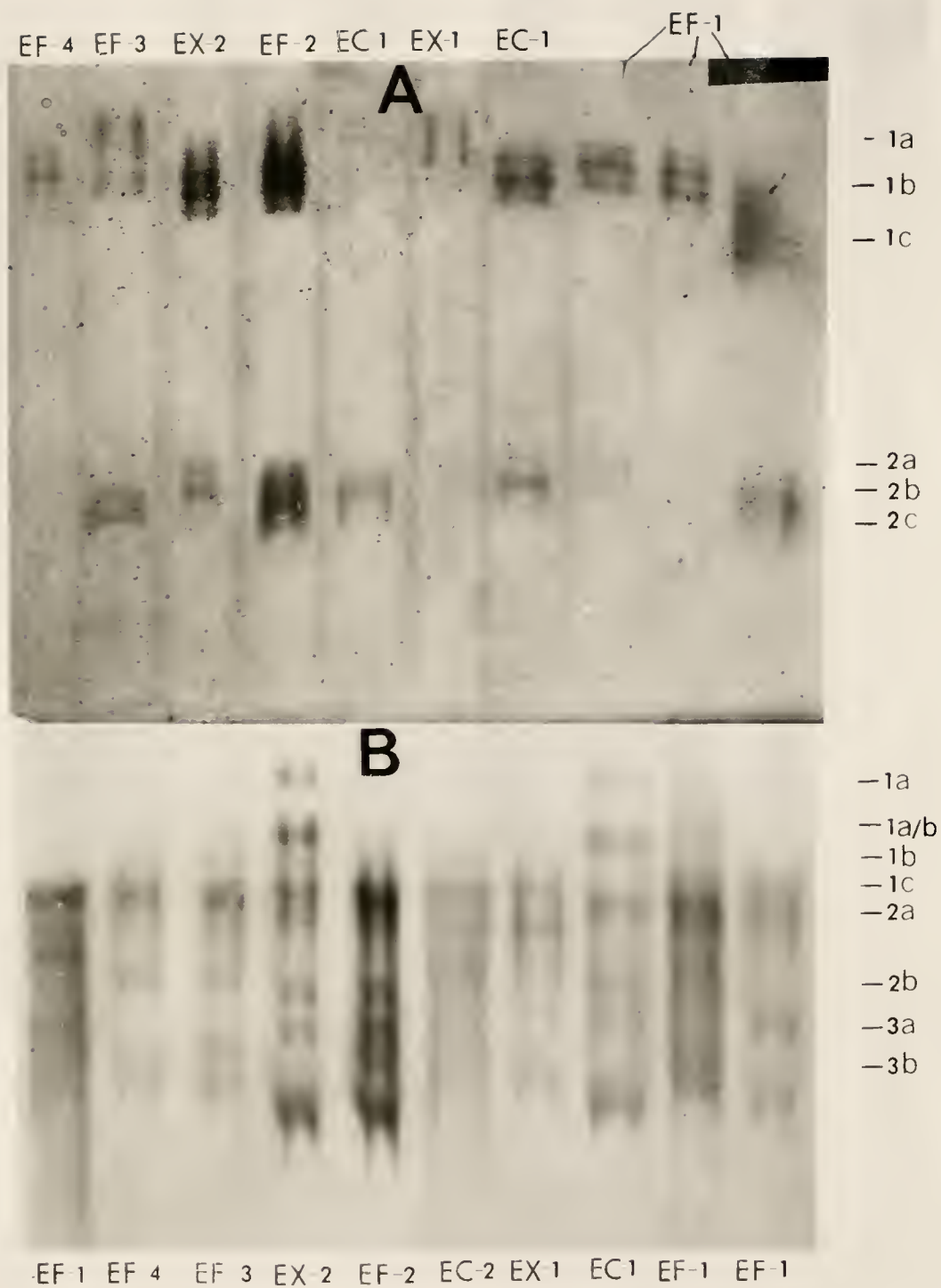
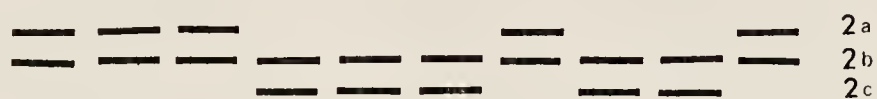
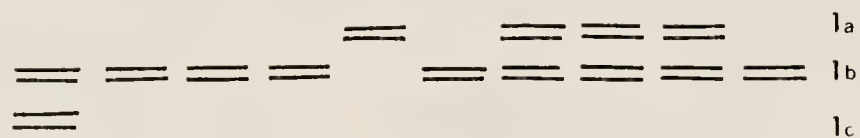
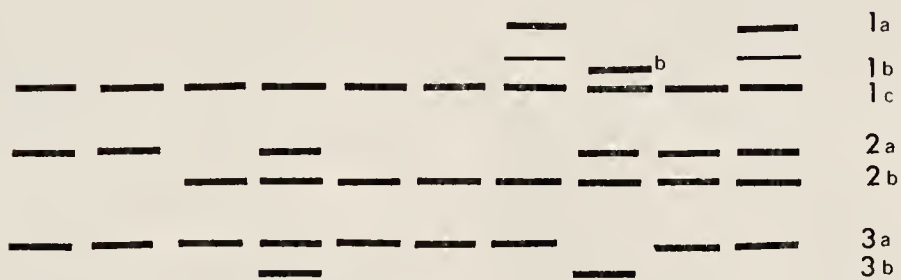


Figure 8.6. Electrophoretic phenotypes at all polymorphic loci in the Eucharis candida/formosa complex. Numbers and lower case letters to right refer to loci and alleles respectively. Refer to Table 2 for population designations. AAT = aspartate amino transferase, MDH = malate dehydrogenase, GSSGR = glutathione reductase, SKDH = shikimate dehydrogenase.

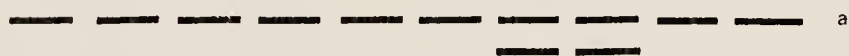




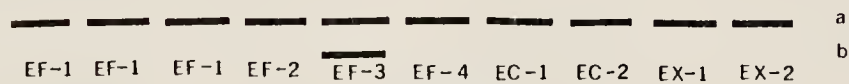
**AAT**



**MDH**



**GSSGR**



**SKDH**

Figure 8.7. Cluster analysis dendrogram of Eucharis bouchei complex based on Nei (1972, 1978) distances.  
Refer to Table 1 for population designations.

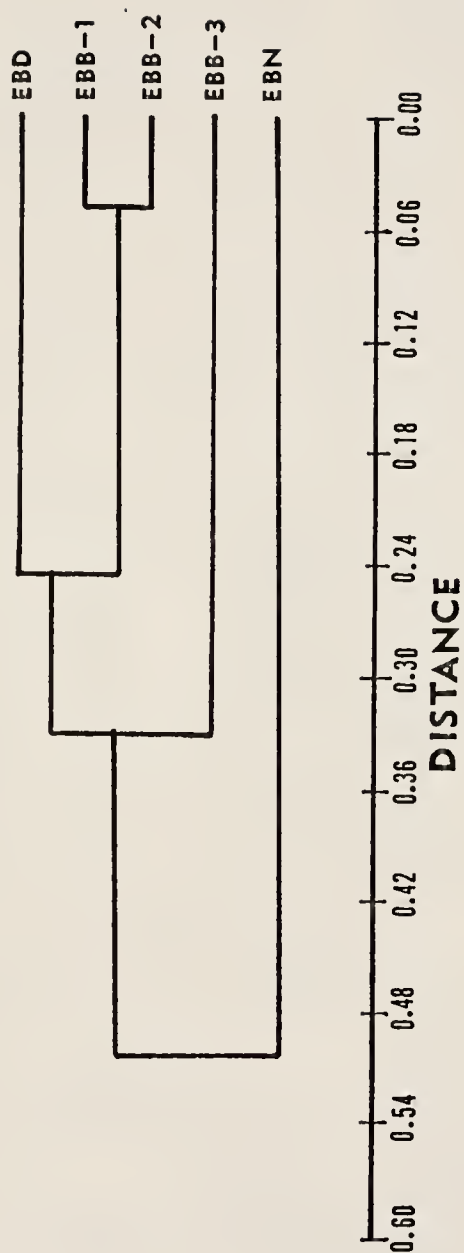
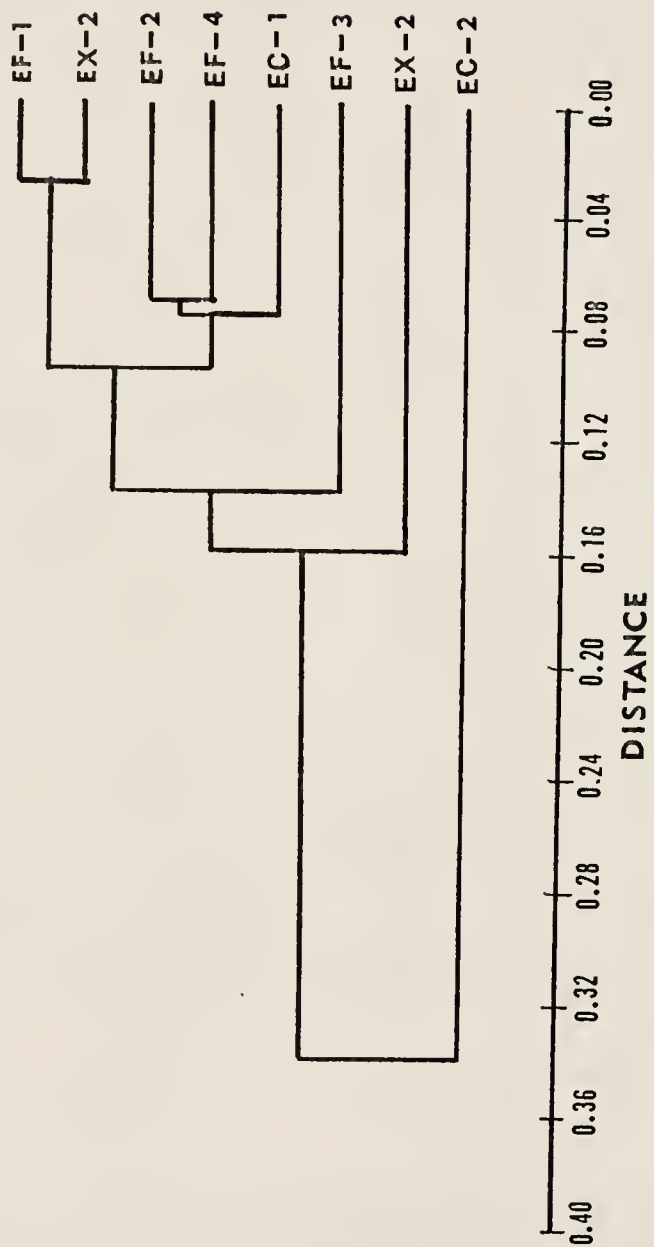


Figure 8.8. Cluster analysis dendrogram of Eucharis candida/formosa complex based on Nei (1972, 1978) distances. Refer to Table 2 for population designations.



CHAPTER IX  
ECOLOGY, PHENOLOGY, AND PHYTOGEOGRAPHY

Ecology

Eucharis and Caliphruria are both strongly mesophytic. All species exhibit high fidelity to a primary forest niche, and severe disturbance of the forest canopy is probably catastrophic to these plants. In recently cleared forest sites, the bulbs persist for a few seasons, but the leaves developed in sunlight exhibit chlorosis and necrosis (pers. obs.). Wilkins (pers. comm.) reports that leaves of E. amazonica are damaged at light levels above 5000 foot candles, an observation confirmed by Rees (1985). Fidelity of these genera to mesic, low-light habitats suggest a strongly evolved adaptive complex. Initial colonization of these habitats may have been the primary factor in divergence of the ancestral eucharoid complex from the rest of the Pancratioidinae. Only two other genera of pancratioid Amaryllidaceae are completely adapted to forest understory: Eurycles, a small Australasian genus; and Urceolina, sister group to Eucharis and Caliphruria (see Chapter XI).

Eucharis is often prevalent in low-lying flood plain sites or creek beds where frequent short-term inundation is likely. Eucharis castelnaeana is almost always encountered on seasonally inundated soils. Access to a population of E. plicata in the vicinity of Tocache Nuevo, Peru, which I studied in July 1982, was precluded on one occasion by



flooding. Largest populations of any species are usually associated with flood plain colonization, though many species are found in more upland sites in less abundance. No fully deciduous species of subg. Eucharis have been observed, though E. astrophiala, endemic to the western slopes of north-central Ecuador, does enter a season of dormancy when growth ceases. However, several leaves may persist for the duration.

The rarity of Eucharis and Caliphruria species throughout their range is a striking characteristic of their distribution. Single, widely-dispersed clumps of bulbs are more the rule than the exception. Herbarium specimens are usually unicate collections, and often indicate the relative infrequency with which the plants were encountered in the forest. The largest population of Eucharis that I have observed consisted of about fifteen clumps of bulbs of E. anomala in an approximate half-hectare area. Throughout eastern Ecuador, populations of only 2-3 genets (and frequently as low as one) of E. candida, E. formosa and E. anomala are the norm. In eastern Peru, a careful search through a five hectare area turned up only two plants of E. cyaneosperma. Edaphic conditions are probably important factors limiting colonization and establishment of Eucharis species. Restriction to sites of high fertility is evident for all species of Eucharis, and has been noted by floristic workers in the Amazon basin and Chocó region of Colombia (Gentry, pers. comm.). The low percentage of fertile rainforest soils is a well known fact of tropical ecology (Richards, 1968). In most upland sites, where the recurrent silt deposition characteristic of flood plains is absent, Eucharis are much more widely dispersed, single-bulb clumps are more frequently

encountered, and these are usually restricted to pockets of humus accumulation at the bases of trees. Large populations of Eucharis may therefore be potential indicators of soil fertility in the Amazon basin.

The overwhelming majority of collections of subg. Eucharis is from elevations below 1000 m and, of these, more than half are below 500 m. Ecology of subg. Heterocharis suggests affinity with that of subg. Eucharis. Collections of E. sanderi are from sites between 50 and 500 meters in very wet, lowland rain forest. Eucharis anomala and E. amazonica occur at higher elevation, between 500 and 1500 m. Caliphruria is primarily collected at sites above 1000 m ("selva-subandina" of Cuatrecasas, 1958). Most collections of Caliphruria (C. subedentata) were from the Río Cauca River valley of western Colombia, an area now largely deforested. In July, 1984, I was not able to find members of this genus in any of its historical localities. The leaves of Caliphruria appear smaller and slightly thicker than those of most species of Eucharis. At least one species, C. tenera, is deciduous, suggesting possible adaptation to water stress. This may reflect adaptation to the leeward montane forests of the Colombian cordilleras, which are drier than their counterparts on the Amazonian and Pacific slopes (Cuatrecasas, 1958).

### Phenology

Eucharis and Caliphruria species show a degree of seasonality in flowering. Very well-collected species, such as E. candida or E. formosa, show flowering patterns skewed toward certain months (January to March), but at least several flowering collections have been made

throughout the year. Species in Amazonian Peru have been collected in flower most frequently from June to September. Each inflorescence is moderately long-lived, from 2-3 weeks, but usually no more than 1-3 flowers are open at any one time. Anthesis occurs the first day the flower opens. All but one species (E. castelanaeana) are protandrous. The style continues to elongate during the first and second day following anthesis. Stigma expansion and receptivity does not occur until late in the second day after anthesis or on the third day. By this time, anthers have begun to senesce. The perianth may remain in good condition for four days following anthesis, but the onset of senescence has been observed to coincide with stigma receptivity in a number of species. Successful greenhouse pollinations have been accomplished after the onset of perianth senescence.

Mass flowering in nature is characteristic of a single species, E. castelnaeana. This species is also the only autogamous species yet known. Eucharis castelnaeana forms large colonies of offset bulbs, most of which flower synchronously. Most other species, even if large numbers of offset bulbs have formed, produce their inflorescences sporadically or successively in their natural habitat. In cultivation, however, some clones of these same species will occasionally flower synchronously.

On the basis of observing greenhouse collections over a five year period, an annual flowering pattern appears characteristic of most Eucharis and Caliphruria species. Eucharis amazonica, however, flowers 2-3 times during the year. Van Bragt and Sprenkels (1983) have regularly induced flowering in this species at any time of the year after treatment at 27<sup>0</sup> C for at least 2 weeks. Collection data for this

species throughout its narrow range indicates that this phenology may occur in habitat as well. Eucharis castelnaeana mass-flowers in the greenhouse twice per year, but its behavior in habitat is unknown. Other well-collected species (e.g., E. candida and E. formosa), which show a peak period of flowering in certain months, are probably annual flowering, with some populations, or individuals in a population, flowering earlier or later. Where abundant offset bulbs have formed, successive replacement (with some overlap) of one inflorescence with another may create a flowering duration of 2-3 months for any one individual clump of bulbs. A population of E. plicata and putative hybrids with E. ulei was surveyed in the middle Río Huallaga valley of Peru. Out of thirteen clumps of bulbs encountered, only two were in flower, one near the end of its cycle, the other near the beginning. A single inflorescence was present in both flowering individuals, even though each consisted of at least four bulbs as large as the flowering offset. Five individuals were in fruit, the capsules fully mature and dehiscent. The remaining individuals were sterile. This heterogeneity may be a reflection of the hybridity of this population, and therefore atypical.

Bawa (1983) reviewed the subject of flowering phenology in tropical plants. Most of the work to date on this subject involved woody canopy species, particularly in the seasonally dry tropics. Rainforest understory plants have been the subject of only a few studies [e.g., Stiles, 1975 for Heliconia (Heliconiaceae)]. For lowland, wet forest species of the tropics, biotic factors such as availability of pollinators, are probably more important selective forces on phenology than abiotic factors (e.g., photoperiod, seasonality of precipitation).

Bawa (1983) states that rare or patchily distributed plants should have one of two flowering patterns. They may either flower massively (cf. E. castelnaeana), or else each individual may produce a few flowers at one time, but synchronously with other conspecific individuals. The latter pattern may be characteristic of the more common Amazonian species of subg. Eucharis (e.g., E. candida, E. formosa, E. ulei). The latter pattern would fit the hypothesis that most species of subg. Eucharis are trap-lined by female euglossine bees (Chapter X).

### Dispersal

The leathery, bright orange fruit of Eucharis subg. Eucharis is a major apomorphy that defines the subgenus. At dehiscence, the contrast between the capsule and the lustrous black or blue seeds creates a striking visual display. This type of display suggests that fruit and seed function mimetically to attract avian dispersal agents (sensu van der Pijl, 1981), but no confirming observations have been recorded.

Viable seeds of Eucharis also float (pers. obs.), and flood plains are conspicuous sites of successful colonization of a number of Amazonian species. Species distribution patterns (see Chapter XII) show a marked decline in collections upstream from centers of distribution. Thus mechanical dispersal of seeds along watercourses may also be an important agent of species promulgation. For species of E. subg. Heterocharis and Caliphruria, and the single species of subg. Eucharis (E. castelnaeana) that lack the mimetic fruit morphology, this form of passive dispersal may be the major method by which seeds are distributed. Bulbs may function as propagules in this manner as well.



I collected several bulbs of E. candida in the Oriente of Ecuador which were loosely established in the bed of a small creek. The bulbs were fully exposed, but roots had penetrated a short distance into the silt of the creek bottom. Man has undoubtedly contributed to the distribution of several species in the Amazon basin (see Chapter XII). In one case of sympatric species (E. candida and E. formosa), population structure may largely be a result of human agency.

### Phytogeography

Eucharis subg. Eucharis occurs in lowland rain forest sites, primarily on the eastern slope of the Andes. The majority of species are concentrated along the Amazon and its main tributaries, e.g. the Napo and Pastaza system in Ecuador and the Huallaga of Peru (Chapter XII). Eight of the thirteen extant species of subg. Eucharis are endemic to the premontane Andean-Amazonas interface, but no species has been reported east of 68° W longitude. Thus the genus appears to be absent from the great, largely Brazilian expanse of lowland Amazonas. Four species are peripheral isolates from the premontane Andean-Amazonian center of distribution. Eucharis corynandra, very closely related to E. castelaneana and E. plicata, and E. oxyandra, of uncertain phylogenetic relationship, are both known only from the "ceja de montaña" forest formations of north-central eastern Peru. Eucharis astrophiala is endemic to a relatively small area of western Ecuador. Eucharis lehmannii, also of uncertain phylogenetic relationship, is restricted to western Colombia. All peripheral isolates of subg. Eucharis show some degree of morphological novelty (see Chapter XII).



The two species of subg. Eucharis which occur above 2° N latitude are both tetraploid. Eucharis bonplandii, endemic to the Cordilleras Oriental and Central of Colombia is rare and infrequently collected. The Eucharis bouchei complex, a series of geographically isolated and morphologically distinct population clusters, is endemic to Central America, chiefly Panama. Stebbins (1985), in a recent review of polyploidy, found a correlation between high frequency of polyploidy and patchy geographical (or ecological) distributions, coupled with the occurrence of secondary contact between these differentiated populations. Levin (1983) discussed how chromosome doubling may " 'propel' a population into a new adaptive sphere." Though E. bouchei does not exhibit any noticeably novel ecological adaptations, its success in colonizing the Isthmus may have been aided by its polyploid-related genetic diversity. Isozyme patterns reveal a very high level of heterozygosity among tetraploid Eucharis (Chapter VIII). Central American Eucharis are discussed further in a separate subsection of this chapter.

Subgenus Heterocharis is widely dispersed from Colombia to Peru, but each of three species are narrowly distributed. With the exception of a single collection from northern Peru, E. anomala is not found outside of Ecuador. It is the only species of Eucharis found on both sides of the Andes. This latter fact is particularly significant in view of the cladistic hypothesis that E. anomala is the most primitive species in the genus. Eucharis amazonica is found natively within a narrow area of the Río Huallaga valley in Peru. Eucharis sanderi is endemic to the Chocó region of Colombia.

Caliphruria is almost completely western Colombian, most prominently in the Río Cauca valley, with a secondary distribution in the Río Magdalena valley. A single species, C. korsakoffii, is Peruvian.

#### Phytogeography of Eucharis and the Pleistocene Refugia Theory

Pleistocene events now substantiated in the literature have undoubtedly influenced the evolution of Eucharis and Caliphruria. Simpson (1971), Van der Hammen (1974) and Prance (1978, 1982a, b) summarize much of this work. Their consensus is that both montane and lowland rain forest were fragmented during Pleistocene glacial periods due to prevailing xeric climatic trends, and subsequently re-expanded during interglacial pluvial periods. Furthermore, montane vegetational belts were lowered during glacial periods. The second process would have had relatively little effect on taxa in question, as neither Eucharis or Caliphruria inhabit vegetation belts above 2000 m. The sum effect of the lowering of Andean vegetational zones on Eucharis and Caliphruria would have been reinforcement of isolation previously imposed by initial uplift of the Andes. The former process, however, would have enormous impact on organisms tied to a rainforest habitat.

The result of much biogeographic work since that of Haffer (1969) has been the construction of an elaborate Pleistocene refugia theory for the Neotropics. This work is summarized in Prance (1982a, b). Prance (1973) provided the first phytogeographic support for the Pleistocene refugia theory in the Amazon basin. He favored Haffer's (1969) idea concerning the distribution of refugia, but expanded their limits considerably (Fig. 1). Prance (1982a) has since further amended size

limits and distribution of proposed refugia. When distributions of extant Eucharis and Caliphruria species (Chapter XII) are superimposed upon proposed refugia sites, several striking correlations become evident. The distribution of Caliphruria subdentata is included in or occurs marginally to the Chocó refugium of Haffer (1969) and Prance (1973, 1982a). Eucharis sanderi (subg. Heterocharis) is endemic to the area of the Chocó refuge. Caliphruria is relatively species poor (4 species). This may be partially a consequence of present limits of wet forest habitats in western Colombia conforming largely to the limits of the Chocó refugium. In other words, the Chocó refugium has never experienced secondary contact with other rain forest refugia during interglacial expansion phases. The occurrence of hybridization between E. sanderi and C. subdentata (X Calicharis butcheri) may reflect a pattern of fragmentation and coalescence that occurred within the limits of the Chocó refugium, a hypothesis recently put forth by Gentry (1982b). Caliphruria is also represented by two rare species in the Río Magdalena valley of Colombia (C. hartwegiana and C. tenera), and one equally rare species in northern Peru (C. korsakoffii). The Río Magdalena species show close phenetic relationship with C. subdentata of the Río Cauca valley, particularly on the basis of pollen exine morphology (see Chapter V), but Peruvian C. korsakoffii has both different pollen and unique leaf surface morphology. It is unclear if Caliphruria was at one time much more widespread in northern South America, and has since suffered drastic reduction, or if C. korsakoffii represents the result of a long-distance dispersal event.

Two areas of greatest taxonomic complexity in subg. Eucharis are evident, the Napo-Pastaza river system of Ecuador and Peru, and an area

in east-central Peru consisting of the lower Río Huallaga valley below 800 m. The former conforms to a refugium so named by Haffer (1969), although Prance's (1973) expanded concept of the Napo refugium seems to correspond better to phytogeographic study of subg. Eucharis. All of the Oriente of Ecuador is contained within the limits of the Napo refugium. Eucharis candida and E. formosa are the only two species of Eucharis found in eastern Ecuador north of the Pastaza valley. Most of their occasional occurrences in Peru and Colombia either fit within either one or the other of Prance's (1973, 1982a) proposed limits of the Napo refugium, or are closely peripheral. A few outlying collections from the middle Río Huallaga valley in Peru do not fit any proposed refugium. These species are often sympatric, and present a complex mosaic of morphological variation from herbarium specimen examination alone. They do show a measure of phenetic differentiation (Chapter VI), but patterns of genetic variation are complicated (Chapter VIII), and hybridization between them seems to have occurred. This may reflect a pattern of secondary contact between populations, vectored by successive fragmentation and coalescence of subsidiary refugia within the limits of the Napo refugium.

Eucharis cyaneosperma and E. ulei are two sibling species both morphologically and cytologically close. Eucharis ulei is concentrated in northern Peruvian Amazonas, while E. cyaneosperma has most frequently been collected in the southern half of Peru and contiguous Bolivia. These two taxa may represent the results of allopatric speciation within a formerly continuous ancestral complex, vectored by isolation within refugia. Most present day populations of both species are found either in the Napo and East Peru refugia of Prance (1973) or the Peru-Acre

refugium of Prance (1982a). The limits of Prance's (1982a) Beni refugium would have to be expanded to allow congruence between it and present-day occurrence of both taxa in Bolivia. However, as with the E. candida/formosa complex, rare occurrences of both species in the middle Huallaga valley of Peru are not congruent with any proposed refugia.

The two subspecies of Eucharis plicata also show phytogeographic patterns that may have been influenced by Pleistocene refugia. Eucharis plicata subsp. brevidentata, the least derived of the two subspecies morphologically, is presently known from only two localities: Amazonian Bolivia and north-central Peru (Amazonas Department). The Peruvian locality is at the very periphery of Prance's (1973, 1982a) Napo refugium. The Bolivian locality would fit an expanded concept of the Beni refugium (Prance, 1982a). However, Eucharis plicata subsp. plicata is a narrow endemic known only from a small area in the middle Río Huallaga valley of Peru.

It is thus apparent that the middle Río Huallaga valley of Peru, while a major locality for Eucharis species, and with at least three endemic taxa (E. amazonica, E. bakeriana, E. plicata subsp. plicata), does not fit the limits of any worker's proposed refugia sites. Further evidence of isolation of Huallaga Eucharis populations from other clusters of species occurrence is the cytological (Chapter VII) and genetic (Chapter VIII) divergence of Huallaga E. formosa from Ecuadorean populations of this same species. These data are thus good evidence for hypothesizing a Huallaga rainforest refugium in east-central Peru (Fig. 1).



Eucharis in Central America

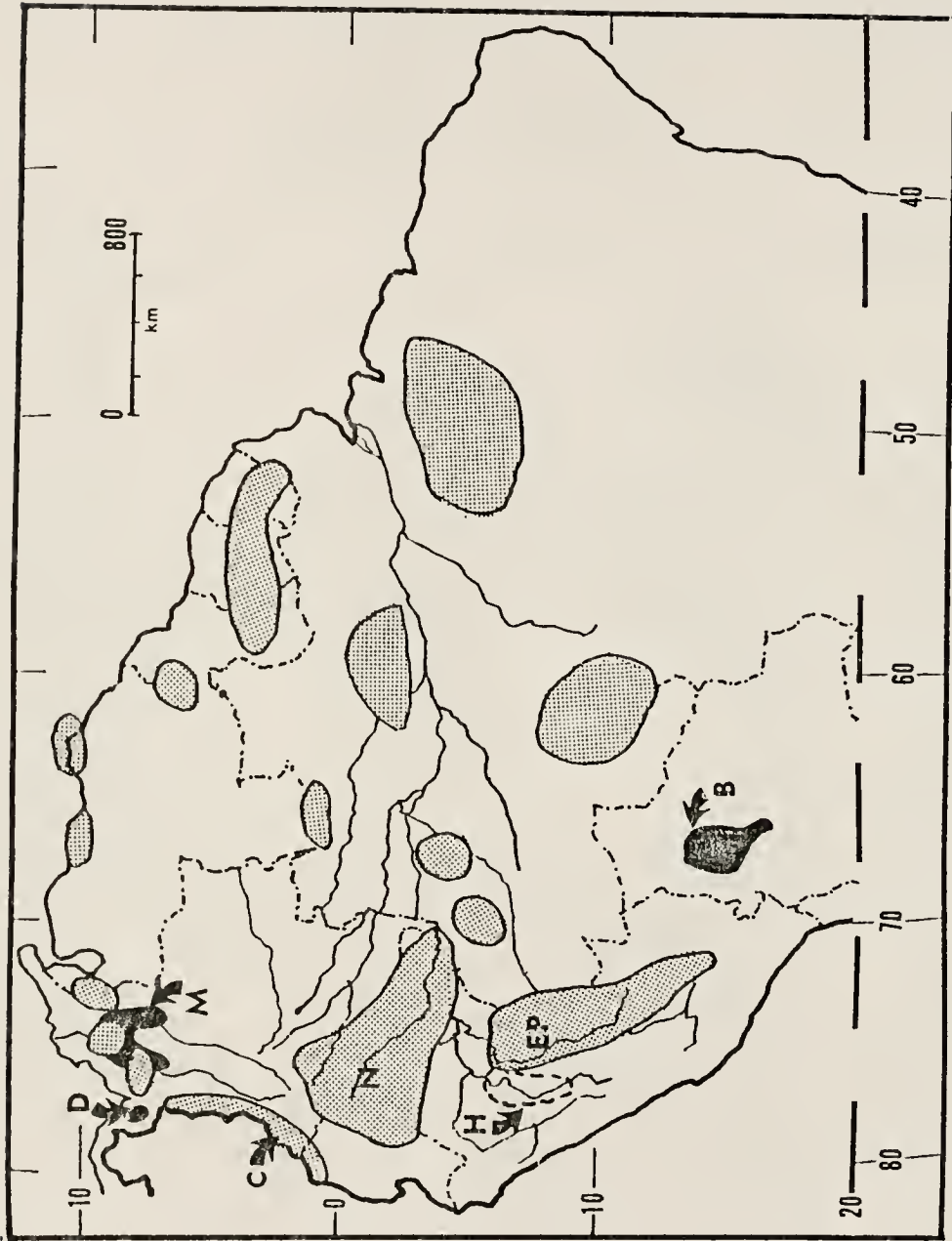
Gentry (1982a) suggests that two major opportunities, widely-spaced in time, existed for floristic interchange between Central and South America. The first, occurring during the Late Cretaceous, was limited to a series of volcanic islands (the proto-Antilles; Dengo, 1975; Lillegraven et al. 1979). The degree to which this island arc remained above water is unknown. At the beginning of the Tertiary, however, this link between the continents was disrupted as the proto-Antilles began a northward displacement. It was not until the late Tertiary that the second opportunity for floristic interchange began to coalesce, as formation of the Central American trench and new volcanic activity gave rise to a new series of islands. These islands eventually formed lower Central America, with a land bridge across the Isthmus of Panama firmly established in the Pliocene, only ca. 3 million years ago (Keigwin, 1978; Marshall et al., 1982). Gentry (1982a) concludes that only very well-established Cretaceous taxa would have been able to take advantage of the earlier connection via island-hopping. Entries into Central America dating from this earlier connection, would be expected to show strong taxonomic differentiation in Central America. Gentry (1982a) cites tribe Crescentieae of the Bignoniaceae as a putative example of early colonization of Central America by island-hopping, followed by taxonomic differentiation. On the contrary, any migration dating from the Pliocene or Pleistocene, would not be expected to show much differentiation, either at the specific or generic level. I have characterized the Eucharis bouchei complex as a semi-species complex of geographically-isolated races or varieties not yet strongly differentiated (Chapter XII). Patterns of genetic variation (Chapter



VIII), chromosome cytology (Chapter VII), and morphological variation (Chapters VI and XII) in this group suggest that the entry of Eucharis into Central America was a fairly recent event.

The species of subg. Eucharis geographically closest to E. bouchei, is E. bonplandii, a rare taxon of central Colombia, and also tetraploid. It is inconclusive whether these two species represent a monophyletic, tetraploid group. Nonetheless, the congruence of phytogeography with chromosome number in these two taxa suggests that this may indeed be the case. It is tempting to speculate if tetraploid Eucharis were at one time more common in northern Colombia, and that E. bouchei and E. bonplandii represent the remnant populations of a once more widespread ancestral, tetraploid complex. Prance's (1982) most recent distribution of Pleistocene refugia based on phytogeographic patterns includes both a Río Magdalena refuge in northern Colombia (most collections of E. bonplandii are from the Río Magdalena valley, though further south of Prance's proposed refuge), and a Darién refuge in southwestern Panama (Fig. 1). Eucharis bouchei var. darieniensis is most common in the area of the Darién refuge, and is putatively the least derived variety of the species. The absence of collections of Eucharis subg. Eucharis from northern Colombia is something of a mystery, but may indicate that extinction of intervening populations between E. bonplandii and E. bouchei was widespread in the recent geological past.

Figure 9.1. Pleistocene refugia in northern South America proposed by Prance (1973, gray; 1982a, black). Dotted line indicates proposed Huallaga refugium in Peru (see text). Only refugia discussed in the text are labelled. B = Beni, C = Chocó, D = Darién, EP = East Peru, H = Huallaga, M = Magdalena, N = Napo.



## CHAPTER X REPRODUCTIVE BIOLOGY

### Pollination Biology

Data on pollination ecology of Amaryllidaceae in general are scant, and represent an area sorely in need of investigation. No information on pollination of Caliphruria is available. The large, white, heavily and sweetly fragrant flower of E. amazonica (subg. Heterocharis) was considered a model moth-pollinated flower by Percival (1965). She noted that the nectar level in the tube rises to a maximum height of 23% tube length, thus effectively preventing access to all but long-tongued insects. Pollination of flowers of subg. Heterocharis, the most ancestral complex of species in Eucharis, by sphingid moths may be the primitive state in the genus. Other basal genera (sensu Meerow, 1985) of "infrafamily" Pancratioidinae also are specialized for hawkmoth pollination (Hymenocallis: Bauml, 1979; Grant, 1983; Pancratium: Morton, 1965).

Floral fragrance, characteristic of all three species of subg. Heterocharis, is rare in subg. Eucharis, occurring in only four taxa, E. bakeriana, E. castelnaeana, E. formosa and E. plicata subsp. brevidentata. However, floral fragrance is only weakly developed in these species, and in one of them (E. formosa), the odor is slightly fetid. Vogel (1963) reported euglossine bees visiting Eucharis "bankeriana" (= bakeriana N. E. Britton?). Visitation by an

unidentified euglossine has been reported for other, unidentified species of subg. Eucharis in Peru (J. Schunke, pers. comm.). In addition to the majority of the species in this subgenus lacking fragrance detectable to humans, the shorter perianth tubes of these species may allow availability of nectar to bees or other insects. I have observed the nectar level rising to the perianth throat in small-flowered taxa of subg. Eucharis. The staminal cup of the flower, exerted beyond the spreading limb could conceivably present a landing platform for insects incapable of hovering (M. Whitten, pers. comm.). What may have begun as purely facultative visitation by bees may in turn have become a selective force within Eucharis for smaller flower size and reduction in fragrance. Many bees are capable of detecting floral fragrances unnoticeable to humans (Percival, 1965), however, and they reportedly visit Peruvian species of subg. Eucharis.

Janzen (1971) discussed the potential long-distance pollination activities of female euglossine bees in the lowland neotropics. Females were observed to fly as much as 23 km in search of pollen and nectar reserves for brood-rearing. Janzen coined the term "trap-lining" to describe the behavior of these insects when foraging. He hypothesized that female euglossines would visit spatially dispersed flowers along a memorized flight pattern through the forest each day. He further suggested that such trap-lining behavior would promote outcrossing among tropical plants of low population density, and perhaps insure the survival of such rare or spatially restricted plants.

The phenology of Eucharis (rarely more than 1-2 flowers open per inflorescence at any one time over a period of 1-2 weeks, and the often successive appearance of inflorescences from a clonal clump of bulbs)

and the dispersed distribution of plants in the wild, suggest that these plants are pollinated by such trap-lining organisms. That the only recorded observations of visitors to Eucharis are for euglossine bees, further supports this hypothesis. The tendency towards synchronized blooming among conspecific populations would at least strengthen the probability that conspecific flowers would be encountered in any one foraging bout. However, congruence of flowering period between sympatric species, as is the case with E. candida and E. formosa in Ecuador, might result in instances of interspecific hybridization. This appears to have occurred at times, not only among the former species, but between E. plicata subsp. plicata and E. ulei in Peru as well. If ecological constraints force convergence in flowering period among sympatric populations of different species, one might then expect selection pressures to exert themselves in other ways that might influence pollinator specificity. In this regard, consistent flower size differences between E. candida and E. formosa, as well as the presence of floral fragrance in E. formosa and its absence in E. candida, may be significant.

One species of Eucharis subg. Eucharis exhibits a very different flowering pattern. Eucharis castelaneana, the smallest-flowered species in the subgenus, vigorously forms large clonal clumps which mass-flower, perhaps biannually. The flowers are also mildly and sweetly fragrant. Furthermore, E. castelaneana appears to be functionally autogamous. This species may therefore be visited by more local insect pollen vectors attracted by the mass display and olfactory cues.



### Breeding System

Most species of Eucharis and Caliphruria appear to be self-incompatible on the basis of greenhouse pollination studies with both pollen of the same flower and inter-flower pollen (geitonogamy). This observation, and the high levels of heterozygosity found in the genus (see Chapter VIII), suggest that most species are predominantly outcrossing. Further evidence of outcrossing is the marked protandry of Eucharis flowers, and the presence of natural interspecific hybrids in the wild. Of all species tested, only E. castelnaeana regularly sets capsules with self-pollen, and stigma receptivity of this species coincides with anthesis. Capsules are set readily with sibling pollen on all species (including E. castelaneana) with the exception of functionally sterile hybrid taxa (E. X grandiflora, X Calicharis butcheri) and E. amazonica. This latter species, probably triploid derived and with ca. 50% pollen inviability, has not set capsules with self, sibling, or interspecific pollen. M. D. Williams (pers. comm.) reportedly induced fruit set with pollen of Hymenocallis and Hippeastrum pollen, but the resulting seed was inviable.

The self-incompatibility (SI) system of Eucharis is unknown. Two character states of Eucharis (dry-type, papillate stigmas and reticulate exine) have been correlated with sporophytic SI in other plants. (Heslop-Harrison and Shivanna, 1977; Zavada, 1984). However, according to several workers, sporophytic incompatibility is unknown in monocots (Heslop-Harrison, 1976; Kress, 1981; Larsen, 1977).

The putative presence of SI in Eucharis is not in concordance with limited data for other rainforest understory plants. Kress (1983) found

full self-compatibility in the majority of 19 Costa Rican Heliconia species tested, and cited unpublished data of Grove, who found similar results in a broader survey of understory plants. However, Bawa and Beach (1983) tested 14 species of woody Rubiaceae in Costa Rica, most of which were found to be self-incompatible. Self-incompatibility is also characteristic of most canopy tree species in the tropics that have been tested (Arroyo, 1976). Kress (1983) suggests that the availability of long-distance pollinators and low daily output of flowers may enforce outcrossing among otherwise self-compatible understory plants in the tropics. Eucharis exhibit this type of phenology, are putatively pollinated by trap-lining female euglossine bees, but are nonetheless at least partially self-incompatible. Perhaps self-incompatibility is an ancestral state in Eucharis (all other genera of Pancratioidinae that I have tested will not self), and has persisted in all outcrossing species despite a lack of selective pressure for its genetic maintenance.

Under greenhouse cultivation, some species of Eucharis, which otherwise do not set fruit with self-pollen, will set capsules late in the flowering cycle, even when no other inflorescences are available for insect-vectored pollen transfer. If anthers are removed from all flowers before anthesis, fruit formation will not occur. This suggests that only partial-incompatibility (Leffel, 1971; Pandey, 1959) may occur in Eucharis. The ability to set fruit with self-pollen (perhaps limited to geitonogamous pollen) late in the flowering cycle may serve as a "fail-safe" measure in the absence of inter-plant pollen transfer. Though agamospermy cannot be ruled out, tests for apomixis have been inconclusive. Fruit set has never occurred on flowers from which the

stigma and style has been excised. However, apomixis can be pseudogamous (Focke, 1881), thus requiring pollination.

Autogamy in E. castelnaeana is associated with a number of other divergent character states for subg. Eucharis. This species has a mass-flowering phenology; the smallest flowers in the genus; a green, often tardily-dehiscent capsule; a less-turgid seed with a dull, rugose testa; and telocentric chromosomes. The most interesting correlation from the standpoint of reproductive biology is between the phenology of E. castelnaeana and autogamy. The mass-flowering habit of this species is a unique characteristic for the subgenus, and suggests that pollinating agents for this small-flowered taxon are other than trap-line foragers. Eucharis castelnaeana occurs in geographic sympatry with several other Eucharis species, most frequently with E. ulei and E. cyaneosperma. The occurrence of E. castelnaeana on seasonally inundated substrates, however, may indicate a degree of ecological allopatry. The evolution of both novel phenology and breeding system may have arisen through competition for pollinators among sympatric congenors, the "reproductive assurance hypothesis" of Jain (1976). Autogamy would insure that a novel phenological pattern would become fixed in a species. If only partial incompatibility exists among Eucharis species, the evolution of complete autogamy in E. castelnaeana could have been relatively rapid. Autogamy would aid the fixation of structural rearrangements in chromosomes as well, a potential isolating mechanism (Jain, 1976). The presence of telocentrics in E. castelnaeana is the best evidence for this. Colonization of seasonally inundated soils appears to be a major adaptation of E. castelnaeana in relation to sympatric congenors.

Inbreeding would allow rapid multiplication of a successful colonizing genotype [the "infective principle" of Stebbins (1950)].

Few barriers to artificial interspecific hybridization have been encountered in greenhouse tests of Eucharis species. However, the autogamous species, E. castelnaeana, would not function as maternal parent in any interspecific cross attempted. Seedlings of a number of putative interspecific and intergeneric crosses (with Caliphruria and Urceolina) are presently in cultivation. Curiously, all attempts to cross Ecuadorean Eucharis species with Urceolina microcrater have failed. Only a single Peruvian collection of E. ulei was successfully hybridized with U. microcrater. Eucharis ulei also shows a measure of karyotypic similarity to U. microcrater (see Chapter VII).

Reproductive biology of Eucharis and Caliphruria is thus still largely unknown. The rarity of the plants is an obstacle to field studies in this area. The disappearance of populations of these genera and their pollinating agents, concurrent with rainforest destruction, can only further impede investigation of this aspect of their biology.

CHAPTER XI  
PHYLOGENETIC RELATIONSHIPS AND EVOLUTIONARY HISTORY

The most recent treatments of the Amaryllidaceae (Traub, 1963; Dahlgren et al., 1985) have placed Eucharis (including Caliphruria, Mathieua, and Plagiolirion) and Urceolina in the tribe Eucharieae (Pax) Traub together with Hymenocallis Salisb., Eurycles Salisb., and Calostemma Brown. The latter two genera are Australasian in distribution and Hymenocallis is entirely Neotropical. Unifying characters of this tribe are 1) presence of a staminal cup, whether conspicuous or reduced, and 2) fleshy seeds. On the basis of anatomical study of the seeds, I do not believe that the globose, turgid seeds of Eucharis and Caliphruria with their characteristic phytomelaneous testa (Huber, 1969) are homologous with the fleshy, bulbiform (and sometimes viviparous) seeds of Hymenocallis, Eurycles and Calostemma. Seeds of these genera [with the exception of two species of Hymenocallis, H. quitoensis Herbert and H. heliantha Ravenna (= Lepidochiton Sealy)] lack phytomelan in the seed coat. Furthermore, the bulbiform seeds of Hymenocallis, and those of Eurycles and Calostemma, have different ontogenetic origins. This is discussed in greater detail in Chapter IV. Consequently, tribe Eucharieae as presently circumscribed is probably polyphyletic. The Eucharieae was recognized as one of four tribes comprising "infrafamily" Pancratioidinae (of subfamily Amarylloideae) by Traub (1957, 1963). Traub's (1963) remaining subfamilies (Allioideae, Hemerocalloideae, Ixiolirioideae) are recognized at the familial level



in recent classifications by Huber (1969) and Dahlgren, et al. (1985), a concept which I follow in my own work. Consequently, "infrafamily" Pancratioidinae could be raised to the status of subfamily. A detailed discussion of these taxa as a distinct evolutionary unit worthy of the rank of subfamily is in preparation. The Pancratioidinae consists of four tribes (sensu Traub, 1963): Euchareae, Eustephieae (Pax) Traub, Pancratieae Salisb. and Stenomesseae Traub. Ravenna (1969, 1974) has shifted some genera to different tribes. Most recently, Dahlgren et al. (1985) combined tribes Stenomesseae and Eustephieae.

Traub (1971) transferred Eucharis, Caliphruria, Mathieua and Plagiolorion into Urceolina without any discussion or supporting data. Mathieua and Plagiolorion are two very poorly known, monotypic genera related to Stenomesson and Hymenocallis respectively (Meerow, MS in submission). However, Eucharis, Caliphruria, and Urceolina appear to form a natural phenetic group defined by characteristics of leaf morphology (petiolate leaf with characteristic cuticular striation, and epidermal cells with undulate anticlinal walls), chromosome number ( $2n = 46$ ), morphology of ovule and seed (turgid, with phytomelanous testa), and ecology (rainforest understory). Before testing this hypothesis cladistically, a review of character states in Urceolina is necessary.

#### A Review of Urceolina

The genus Urceolina Reich. (nom. cons.) consists of perhaps eight species, all restricted to Peru. The relationships of Urceolina have long been misunderstood, most workers (Baker, 1888; Pax, 1888; Hutchinson, 1959) placing Urceolina near Stenomesson Herbert. Traub



(1957) was the first to recognize its affinities with Eucharis. The problem no doubt stemmed from the inclusion of a species of Stenomesson [S. miniatum (Herbert) Ravenna] in Urceolina as U. miniata (Herbert) Benth. & Hook. Despite the ventricose aspect of the corolla morphology of S. miniatum, which is similar to that of Urceolina, the species clearly belongs to Stenomesson as evidenced by its narrow, sub-petiolate leaves, the morphology of its staminal cup, and its numerous flat, black seeds (Ravenna, 1978).

The most striking difference between Eucharis and Urceolina is in floral morphology. Urceolina (Fig. 1A) is easily distinguished by its brightly colored, urceolate corolla formed by the coherence of the tepals throughout most of their length. Vargas (1960) described the genus Pseudourceolina to accomodate a species of Urceolina in which the tepals are more laxly coherent. As in Caliphruria, the staminal cup of Urceolina is reduced to a minute, membranous, basal connation of the filaments which are otherwise linear throughout their considerable length. One or several obtuse teeth may be situated between each stamen. The leaves of Urceolina, in thickness and lack of both surface plication and marginal undulation, resemble Caliphruria more closely than Eucharis. The epidermal cell anticlinal walls of both surfaces are strongly undulate (Fig. 1B, C). Abaxial cuticular striations of Urceolina (Fig. 1D) are very much like those characteristic of Eucharis and Caliphruria (Chapter III), but the striations are thin and slightly less distinct than in Caliphruria. Abaxial epidermal cells of Urceolina are nearly uniplanar (Fig. 1D), whereas in Eucharis and Caliphruria the epidermal cells are strongly raised.

In size the pollen grains of Urceolina (Fig. 1E) are similar to those of subg. Caliphruria. The coarseness of the reticulum is intermediate between that of Eucharis and Caliphruria. In all species of Urceolina the small stigma is capitate and entire (Fig. 1F) versus the trilobed stigma found in Eucharis and Caliphruria. Stigmatic papillae are unicellular as in Eucharis. Urceolina species have from 10-20 ovules (Fig. 1G).

Seed morphology of Urceolina is another major area of morphological divergence from Eucharis and Caliphruria (Fig. 1H-L). The ripe fruit of Urceolina is a thin-walled, yellow-green, turbinate capsule, much like that of Caliphruria. However, the seeds of U. microcrater (Fig 1H) are narrowly oblong, ca. 5 mm long and 1.5 mm wide, and curved. The testa is smooth, lustrous black, and phytomelaneous, with aveolate cell outlines like most Eucharis species. In longitudinal transverse section, an anatomical feature unique to Urceolina is revealed (Fig. 1J, L). At the chalazal end of the seed, a dam of poorly differentiated tissue separates a "cap" composed of many small cells from the endosperm. The cells of the "cap" do not have pitted walls with plasmodesmata as is characteristic of the endosperm cells. There is no obvious surface feature on the seed corresponding to the area of this "cap," and its function is unknown. Elaisomes are found in ant-dispersed seeds of some species of Pancratium (Werker and Fahn, 1975), but these structures appear on the seed surface.

Urceolina also exhibits divergent karyotype morphology (Chapter VII) from most species of Eucharis and Caliphruria. The largest pair of chromosomes in U. microcrater are submetacentric. Whether this characterizes all other species of Urceolina is unknown. The largest

pair of chromosomes are submetacentric in only a single species of Eucharis, E. astrophiala. Chromosomal change correlates with a great deal of phenetic divergence in this species of Eucharis as well.

The distribution of Urceolina appears to overlap with Eucharis only in the vicinity of Tingo Maria in Dept. Huánuco of Peru (Fig. 2), though E. amazonica is the only species of Eucharis found in this area. Urceolina inhabits situations of fast drainage in shady ravines and rock outcrops (Ravenna, 1982; J. Schunke, pers. comm.; Meerow pers. obs.). Altitudinal range of Urceolina is quite variable (700-2000 m). The leaves of at least one species (U. microcrater Krnzl.) are hysteranthous.

The morphology of the flower in Urceolina strongly suggests ornithophily (sensu Faegri and van der Pijl, 1979), i.e., vivid, "parrot" colors, ventricose corolla, pendulous habit, and absence of odor. If this genus is bird-pollinated, mechanical isolation would be an important barrier between it and Eucharis, even in areas of sympatry.

### Phylogenetic Analysis

Phylogenetic analysis (cladistics) has become the standard methodology for testing hypotheses of phylogeny among organisms in systematic biology. The principles of phylogeny inference were formally enumerated by Hennig (1966). A similar methodology, "the Wagner groundplan divergence" method was applied in botany by Wagner (1952, 1962a, b, 1980; see also Churchill et al., 1984) but was overshadowed for many years by Hennig's work.

The philosophical foundation of cladistics, as this form of analysis is called, is based upon certain assumptions of evolutionary thought (Hennig, 1966), that have become axiomatic in their application to this methodology. The first is the concept of monophyletic groups. From the standpoint of cladistic thought (Wiley, 1981), all recognized taxa must be monophyletic, i.e., derived from a common ancestor and including all descendents of this ancestor (but see Ashlock, 1979). Monophyletic groups are recognized by the possession of shared derived characters (= synapomorphies). Shared primitive characters (= symplesiomorphies) cannot be used as a basis for delimiting taxa in a cladistic classification. To do so results in paraphyletic groups, i.e., segregation of one or more descendent taxa from other descendents of their common ancestor (Bremer and Wanntorp, 1978; Hennig, 1966; Wiley, 1981). Polyphyletic groups (more than one ancestry) can result if the characters used to define taxa are non-homologous, i.e., convergence or parallelism has resulted in similar character states evolving along different ontogenetic pathways. Polyphyletic groups are generally considered anathema to phylogenetic thought by cladist and non-cladist alike. On the other hand, some systematists have argued for the acceptance of paraphyletic groups (Ashlock, 1979; Buck, 1986; Dressler, 1986).

Another important concept central to phylogenetic systematics, and perhaps the most controversial, is that of parsimony (Farris, 1970; Farris et al., 1970; Kluge and Farris, 1969). In the context of cladistics, the dictum of parsimony states simply that where two conflicting hypotheses of phylogeny occur, the shortest [i.e., one requiring fewest evolutionary steps or character state changes, and

consequently the fewest number of ad hoc hypotheses of evolutionary change (Wiley, 1981)] is the most parsimonious and therefore the preferable option. Recently, adherents of the character compatibility method of cladistic analysis (see Duncan et al. 1980, and Meacham, 1981 for discussion of this method) have argued that the parsimony method of cladistic analysis is less in accord with Henning's (1966) principles than character compatibility (or "clique") analysis (Duncan, 1984, 1986). Proponents of parsimony have responded vociferously to the contrary (Churchill, et al. 1985; Farris and Kluge, 1985; 1986).

Since accurate cladistic analysis is completely dependent on accurate assessment of homology in characters and polarization of character state changes (i.e., which is ancestral and which is/are derived), rigorous attention must be paid to choosing the characters for the analysis, as well as polarizing the state changes of each. The only phylogenetically acceptable concept of homology is genealogical; i.e, two taxa have the same character because it was present in their common ancestor (Eldredge and Cracraft, 1980). Without a complete fossil record, indirect evidence (anatomical, developmental) is usually all that is available for assessing questions of homology. In cladistic analysis of species of a single genus, homology of characters is usually assured (Wagner, 1980). If the cladogram resulting from an analysis requires that some characters undergo multiple independent origins or reversals, one inference may be that those characters are not homologous.

Despite a lack of consensus on generic and specific limits in Amaryllidaceae, cladistic analysis has only twice before been applied to such problems in the family, by Nordal and Duncan (1984) for Haemanthus



L. and Scadoxus (Raj.) F. Nordal, two closely related, baccate-fruited African genera; and Meerow (1987) for Eucrosia Ker Gawler. Resolution of the generic limits of Eucharis and Caliphruria in relation to Urceolina, as well as interspecific relationships in the former genera, seemed two areas that would benefit from the application of cladistic analysis.

### Materials and Methods

Cladistic analyses were run using PAUP version 2.3 by David L. Swofford (Illinois Natural History Survey), on the Northeast Regional Data Center (NERDC) computer system of the University of Florida. PAUP is a highly versatile package utilizing the "Wagner method" (Farris 1970; Kluge and Farris 1969) of simple parsimony. Due to the high incidence of homoplasy in Amaryllidaceae (Meerow 1985, 1987), the use of the Wagner method, which places no restrictions upon character state changes, seems advisable. All species (and one subspecies) of Eucharis and Caliphruria [21 operational taxonomic units (OTU's)] excluding hybrid taxa were analyzed using forty characters (Table 1, 3).

Character state polarities were assessed via outgroup comparison (Maddison et al., 1984; Watrous and Wheeler, 1981). Out group comparison is the most widely accepted methodology for assigning character state polarities in conjunction with the parsimony method of cladistic analysis. Due to the mosaicism of morphological variation in Andean Amaryllidaceae (Meerow, 1985, 1987), character state polarization is complex and requires some discussion.

### Outgroups, character selection and polarization of states.

Character state analysis preliminary to a cladistic treatment of the



pancratioid Amaryllidaceae (Meerow, 1985) suggests that within the Pancratioidinae, a large, white, fragrant, crateriform flower with a conspicuous staminal cup ("pancratioid," cf. Pancratium), presumably involved with sphingid moth pollination (Grant, 1983; Morton, 1965), may be symplesiomorphic. In other words, while the pancratioid flower was a major apomorphy defining the Pancratioidinae as a distinct group within the Amaryllidaceae, it is the ancestral floral morphology from which all other pancratioid taxa have diverged. I have used the term "the pancratioid base" to define the five genera of Pancratioidinae with this type of flower morphology (Meerow, 1985). These five genera are Eucharis, Hymenocallis Salisb. sens. str., Pancratium L., Pamianthe Stapf, and Paramongaia Velarde. All but Pancratium are entirely neotropical in distribution.

The genus Pancratium (ca. 17 species) and two species of Hymenocallis (H. quitoensis Herbert and H. heliantha Ravenna) were used as the primary outgroups. Character state data on these taxa were accumulated from study of living material, herbarium specimens and various literature (Björnstad, 1973; Meerow and Dehgan, 1985; Morton, 1965; Ponnammma, 1978; Ravenna, 1980; Traub, 1962; Werker and Fahn, 1975). The two species of Hymenocallis are undoubtedly a monophyletic group. They are the only two species of the genus that have phytomelaneous seed coats. These two species have been segregated into a separate genus, Lepidochiton Sealy (1937) on this basis (however, only H. quitoensis was known at that time). The two species are ephemeral components of the xeric flora of southwestern Ecuador and northwestern Peru, and differ only in flower color. Traub (1962) considered H. quitoensis a relict taxon, and the most primitive species of

Hymenocallis. These species of Hymenocallis will be referred to as Lepidochiton in the following discussion. Urceolina, putative sister group to Eucharis and Caliphruria, was included in the analysis to test its phylogenetic relationships to the former two taxa. In this sense, Urceolina is best considered part of the in group for the analysis, since character state polarities were not based on the states occurring in this genus. At times, evolutionary trends in "infrafamily" Pancratioidinae as a whole were used to resolve polarities. This is discussed below wherever such criteria were applied.

All character states occurring in both Pancratioidinae and Lepidochiton were coded as ancestral. Only characters 10 (flower number), 11 (flower color), 36 (seed shape), 37 (testa color), and 40 (chromosome number) could not be polarized using this criterion. Pancratioidinae is putatively the least derived genus of the pancratioid base (Meerow, 1985). Where character states of Lepidochiton and Pancratioidinae were at variance, the state occurring in Pancratioidinae was weighted in judging the ancestral condition for that character.

Flower number could not be polarized with certainty. The hypothesis that the umbellate inflorescence of Amaryllidaceae represents a series of reduced, helicoid cymes (Mann, 1959; Stout, 1944) would suggest that numerous flowers is the ancestral state in the family. Reduction in number would thus represent loss of one or more of the component cymes. Numerous flowers has usually been considered the derived state in the family (Traub, 1962, 1963; Traub and Moldenke, 1949). Nonetheless, to my knowledge, no one has presented any evidence that reversals in this character are developmentally impossible. Uniflory occurs sporadically throughout the family, but several

uniflorous taxa will occasionally produce a two-flowered scape.

Lepidochiton is uniflorous. Two uniflorous taxa also occur in Pancratium. Consequently, both polarities for flower number were tested in the analyses.

A trilobed stigma is also usually considered the ancestral state in Amaryllidaceae (Traub, 1963; Traub and Moldenke, 1949). Nonetheless, both outgroups have a capitate, entire stigma. In this case as well, both possibilities were tried in the analyses.

A chromosome number of  $2n = 22$  is undoubtedly ancestral among extant pancratioid genera (Meerow, 1984). This number occurs among widely unrelated genera of Amaryllidaceae (Flory, 1977). Base number in the Amaryllidaceae is considered by most workers to be  $x = 11$  (Flory, 1977; Goldblatt, 1976; Meerow, 1984). The chromosome number  $2n = 46$ , characteristic of all neotropical pancratioid genera in part or entirely (Di Fulvio, 1972; Flory, 1977; Meerow, 1985, 1987) is likely derived via duplication or fragmentation of a chromosome, followed by doubling of the genome (Lakshmi, 1978; Sato, 1938). Snoad (1952) reported  $2n = 24$  for H. quitoensis. Material I have in cultivation of this species from both Peru and Ecuador has  $2n = 34$  (Meerow, unpubl. data). This number may be triploid derived from the ancestral  $2n = 22$ .

Of the forty characters used in the analysis, 19 were simple, two-state characters. Of the remaining 21 multistate characters, 16 had three states, 3 had four states, and 2 had five states. Some multistate characters were placed into linear transformation series (characters 8, 9, 10, 13, 24, 25, 27, 29, 34; see Table 1). Some of these characters logically called for this type of treatment (e.g., character 34, ovule number). Ordering of other multistate characters

into linear transformation series was based on corroborative trends occurring in other tribes of "infrafamily" Pancratioidinae (Meerow, 1985) or within the family as a whole (e.g., character 28, exine morphology). A number of three state characters (2, 11, 12, 17, 20, 21, 22, 36, 37), and one four-state character (18) were placed into bifurcating transformation series whereby each of the derived states was coded as an independent derivation from the ancestral (Table 1). Finally, character 40 (chromosome number), a five state character (see Table 1), was ordered on the basis of the chromosome data cited above.

### Results

Changing polarities of characters 10 (flower number) and 30 (stigma morphology) did not affect either the topology or the resolution of terminal taxa in the resulting cladograms. The cladogram resulting from the coding the trilobed stigma and few flowers as derived was 134 evolutionary steps long, and had a Consistency Index (Kluge and Farris, 1969;  $CI = \text{total length of cladogram minus homoplasies divided by total length}$ ) of 0.592. The cladogram resulting from the coding of both these characters as ancestral was 135 steps long, with a  $CI = 0.589$ . For the cladogram illustrated (Fig. 3), more than 5 flowers and trilobed stigmas were coded as ancestral. These are the states which I believe are ancestral in "infrafamily" Pancratioidinae as discussed above. This cladogram is 133 steps long, with a  $CI = 0.589$ . It is thus the most parsimonious of the three cladograms, albeit by only a single step. Of the 133 character state changes in Fig. 3, 55 are homoplasies, and 33 are reversals.

As is evident from the cladogram, Pancratium is only one step removed (the evolution of a capitate stigma, homoplasious with Urceolina) from the hypothetical ancestor used to root the cladogram. This is congruent with morphological and karyological data that suggests that Pancratium is the most primitive genus in the Pancratioidinae. According to Traub (1963), a few species of Pancratium do have an obscurely trilobed stigma. Lepidochiton is the next terminal taxon to resolve in the cladogram. Uniflory and 34 chromosomes are the two apomorphies of Lepidochiton, but its hypothetical ancestor is defined by reduction in flower number, globose seeds, and a change in testa color from black to brown. The next internal node of the cladogram is the hypothetical ancestor to Eucharis, Caliphruria and Urceolina, all of which thus form a monophyletic group. Ten apomorphies occur at this node. The most important are the evolution and fixation of the petiolate leaf, the changes in flower habit and pedicel length, tube morphology, pollen size, and increased chromosome number. Rather than an actual reversal to trilobed stigmas, I think it more likely that the primitive state was retained within this monophyletic group until the later divergence of Urceolina.

The next five bifurcations in the cladogram are very interesting. The terminal taxa involved represent Eucharis subg. Heterocharis (E. amazonica, E. anomala, and E. sanderi). It is obvious subg. Heterocharis is paraphyletic. This situation is discussed in detail in the next section. Eucharis anomala also resolves cladistically as the most primitive species of Eucharis, with only two character state changes (crateriform to campanulate perianth, smooth to rugose testa)



defining this species as distinct from the hypothetical ancestor of the eucharoid genera.

Eucharis lehmannii, a poorly known species of uncertain phylogenetic relationship is the next terminal taxon to resolve in the cladogram. The great amount of missing character state information for E. lehmannii compromises its position in the cladogram, but indications are that it may occupy an isolated position between the more primitive and advanced taxa of the eucharoid lineage.

The remainder of the cladogram represents two monophyletic groups. These are Eucharis subg. Eucharis, and Caliphruria and Urceolina respectively. The two apomorphies at the ancestral node are a reversal to numerous flowers, and reversal to shorter staminal teeth.

Eucharis oxyandra, another species of uncertain phylogenetic relationships and a great deal of missing character state information, is placed within the cladogram as ancestral to both Urceolina and Caliphruria. Six apomorphies define this ancestral node: the loss of leaf margin undulation, reduction in flower size, loss of fragrance and androecial pigmentation, reduction in exine reticulum coarseness, and reversal in seed shape. The state occurring in E. oxyandra is known for only two of these apomorphies (flower size and exine morphology). Urceolina has the largest patristic distance of all terminal taxa in the cladogram, with nine apomorphies (leaves hysteranthous, flowers 5-7 cm long and brightly colored, urceolate perianth, anthers versatile at anthesis, long-exserted style, capitate stigma, numerous ovules, and unique oblong, curved seed), four of which are reversals. The hypothetical ancestor of Caliphruria required eight character state changes (straight and green tube, funnelform perianth, long staminal



teeth, finely-reticulate exine, multicellular stigmatic papillae, reduced ovule number, and non-lustrous testa), two of which were reversals. Within Caliphruria, two small, monophyletic subgroups are resolved with two species each. The major differences between these two subgroups is the presence (C. hartwegiana and C. tenera) or absence (C. subedentata and C. korsakoffii) of staminal dentation, and number of ovules.

The large clade comprising Eucharis subg. Eucharis is the monophyletic group in which I have the greatest confidence, since cladistic relationships among the component species confirm relationships based on phenetic and cytological data. Apomorphies at the ancestral node are the reversal to a well-developed staminal cup (more likely the retention of the ancestral state), the extension of androecial pigmentation to both surfaces of the staminal cup, plication of the staminal cup, reversal to shallowly cleft staminal cups (also more likely retention of an ancestral state), the evolution of subulate free filaments (homoplasious with E. amazonica), and the evolution of the bright orange, mimetic fruit. Two major monophyletic subgroups resolve within subg. Eucharis, largely on the basis of staminal cup characters. The first group of species all have shallowly cleft, plicate staminal cups. Within this clade, large-flowered E. bakeriana is the first terminal taxon resolved. The remaining taxa, E. plicata, E. castelnaeana, and E. corynandra are all small-flowered species very close cladistically and phenetically as well (Chapter VI and XII). According to this cladogram, Eucharis corynandra may be ancestral to the former two species. This is doubtful, since two important autapomorphies of E. corynandra (short staminal cup, and club-shaped free filament)

were not included in the character matrix. An ancestor/descendent relationship is also suggested between the two subspecies of E. plicata. All apomorphies expressed in E. castelnaeana are either homoplasies, reversals or both. The most interesting of these is the reversal in this species to an ancestral fruit morphology. A number of the character state reversals that occur in the cladogram could just as likely be considered to be the retention of the ancestral state in that particular clade. I believe that the green, thin-walled capsule of E. castelnaeana may be a true evolutionary reversal, since there is not yet a single additional species of subg. Eucharis that does not have the orange capsule typical of the subgenus.

The second monophyletic subgroup of subg. Eucharis also resolves several possible ancestor/descendent relationships. Eucharis formosa is resolved in a zero-length branch from the ancestral node, defined by apomorphies of plicate leaf lamina and a more deeply cleft staminal cup. The presence of floral fragrance in this species, and its large flower size are symplesiomorphies with E. bakeriana, to which E. formosa also bears close phenetic relationship (Chapter VI). The next terminal taxon is E. candida, also terminating a zero-length clade. Loss of floral fragrance and a reduction in flower size are the apomorphies at this node. The remaining taxa in the cladogram are linked by the following apomorphies: reduction in flower number and ovule number. Eucharis ulei is positioned at the ancestral node. Together with E. astrophiala and E. cyaneosperma, E. ulei forms an unresolved trichotomy in the cladogram. The final monophyletic group within subg. Eucharis is formed by the two tetraploid taxa, E. bonplandii and E. bouchei. Loss of leaf

plication and marginal undulation are the additional apomorphies at the ancestral node.

The cladogram presented in Fig. 3 contains 55 homoplastic character state changes, and 34 reversals. This may raise questions concerning the homology of characters which manifest these changes. Invariably, it is androecial characters (including pollen size) in which a great deal of homoplasy has occurred. The evidence from phenetic studies of Eucharis (Chapter VI) and from study of other genera of the Pancratioid Amaryllidaceae (e.g., Meerow, 1987) indicates that androecial characters are among the most easily modified morphological characters in this group. Not only can species be polymorphic for such characters as staminal dentation (e.g., E. candida, E. formosa, E. ulei, E. oxyandra), but reduction of the staminal cup has occurred independently in every pancratioid tribe, and sometimes more than once (Meerow, 1985, 1987, unpubl. data).

Reduction of the staminal cup is one of seven apomorphies that define a monophyletic group including E. sanderi, E. lehmannii, E. oxyandra, Caliphruria, and Urceolina. Since characters 21 and 22 also included this state, this character --potentially non-homologous among these diverse taxa -- actually represents three of the seven apomorphies at this node. The data matrix was therefore run with characters 19, 21, and 22 deleted. The only change in terminal taxa on the resulting cladogram was that E. sanderi was resolved as sister taxon to E. anomala.

## Discussion

Cladistic analysis indicates that Eucharis, Caliphruria and Urceolina represent a monophyletic group, well-supported by 10 apomorphic character state changes. Within this large group, Eucharis subg. Eucharis forms another clear cut monophyletic group. Cladistic relationships among the species of subg. Eucharis largely corroborate relationships postulated on the basis of phenetic and chromosomal data. The clarity of this clade is due in no small measure to the completeness of the data matrix for the component species.

The sister group relationship between Caliphruria and Urceolina seems to be a very robust cladistic hypothesis. However, three of the four species of Caliphruria are restricted to western Colombia, as is Eucharis sanderi. Hybridization between Caliphruria and E. sanderi, as well as a degree of phenetic resemblance between E. sanderi and Caliphruria led me to earlier hypothesize that subg. Heterocharis and Caliphruria were sister groups, and that Urceolina represented a separate, perhaps even earlier, divergence from the ancestral eucharoid complex (Meerow, 1983). This earlier hypothesis is not supported by the cladogram (Fig. 3).

Of the eucharoid taxa, Eucharis subg. Heterocharis has the greatest number of putatively primitive characters, and clearly represents the more ancestral species in the genus. Nonetheless, my concept of this subgenus is paraphyletic, since descendents of the common ancestor of Heterocharis are excluded from the group. Subgenus Heterocharis is a fairly heterogenous group from the perspective of apomorphic characters alone. Each of the three species may be characterized by autapomorphies, but only symplesiomorphies join them.

By including subg. Heterocharis in Eucharis, Eucharis becomes paraphyletic according to this cladogram.

The cladogram presented in Fig. 4 is a user generated tree picturing relationships from an alternative perspective. In this cladogram, I have positioned Urceolina as an early divergence from the eucharoid lineage, and Caliphruria as a sister group to subg. Heterocharis. The problematic species, E. lehmannii and E. oxyandra, were situated within the clade containing small-flowered species of subg. Eucharis with numerous ovules. This topology of this user-generated tree was then coded and submitted to PAUP along with the character state matrix (Table 3) for analysis of character state changes required to support the topology.

This second cladogram required 154 evolutionary steps, and has a CI of 0.448. Of the 154 character state changes, 85 were homoplasies, and 52 were reversals. Thus, it is less parsimonious than the cladogram in Fig. 3. Since I did not alter the resolution of the species of subg. Eucharis in Fig. 4 from the results pictured in Fig. 3, character state changes supporting its topology are essentially the same in both cladograms. Therefore detailed topology for subg. Eucharis is not illustrated in Fig. 4. The areas of exceptional interest in this user-generated cladogram are the resolution of Urceolina, Caliphruria, E. subg. Heterocharis, and the accompanying character state changes within these clades.

The very early branching of Urceolina from the rest of the eucharoid lineage in Fig. 4, has consequences in the later branching of the monophyletic group composed of Caliphruria and Heterocharis, and further consequences at the ancestral node of subg. Heterocharis. The



ancestral node from which Heterocharis and Caliphruria bifurcate is defined by 4 apomorphies (green tube, curved tube, long staminal teeth, and non-lustrous testa), three of which are reversals. The ancestral node of subg. Heterocharis is defined by nine apomorphies (large flowers, fragrant flowers, reduced flower number, short pedicels, campanulate perianth, versatile anthers, long-exserted styles, rostellate ovaries, and increased ovule number), seven of which are reversals (more likely the retention of ancestral states). If these reversals are actually the retention of the ancestral states in the Heterocharis clade, Urceolina would necessarily require even more apomorphies than the nine indicated in Fig. 4, with an even greater incidence of homoplasy.

The question that must be asked is whether there is any evidence to support such an early divergence of the Urceolina clade from the rest of Eucharis, rather than the more parsimonious phylogeny illustrated in Fig. 3. The only evidence evidence is circumstantial, the vicariant distribution of Urceolina to the south of the center of diversity for Eucharis (Fig. 2). Urceolina urceolata, the southernmost distributed species in the genus, is the largest flowered species of Urceolina, and has the largest number of ovules per locule (20, the ancestral number in the eucharoid line). Assuming the same type of character state changes in Urceolina as in Eucharis, both characters of U. urceolata would indicate that it is a less derived species than U. microcrater (small flowers, 10 ovules per locule), the northernmost distributed species. The greatest diversity of Urceolina is in montane, southeastern Peru. This evidence suggests to me that Urceolina evolved in this region. Relict, ancestral taxa of Eucharis are conspicuously



absent from this geographic region, but are sympatric with more derived species throughout much of the northern range of Eucharis (Fig. 2).

Homoplasy in androecial and pollen characters is widespread throughout the pancratioid Amaryllidaceae (Meerow, 1985), and has been clearly documented within subg. Eucharis alone. Sister group relationships based on such characters are thus suspect. Of the 6 apomorphies at the ancestral node defining Caliphruria, Urceolina and E. oxyandra as a monophyletic group in Fig. 3, two are of this category. Other apomorphies at this node are based on characters of demonstrated plasticity (e.g., leaf characters, flower size) or characters of unknown genetic complexity (seed morphology). Only three apomorphies define Caliphruria and Urceolina as a monophyletic group after the divergence of E. oxyandra in Fig. 3: the habit of the flower, the straight tube, and pollen size. Pollen size, as discussed above and elsewhere in this discussion, is acceptably homoplasious. Flower habit of both genera is actually different (declinate in Caliphruria, pendent in Urceolina) but was coded as a single state on the basis of whether it is a factor of pedicel habit or tube morphology (see Table 1). This leaves the straight tube, a character that may be retention of the ancestral state or a true reversal (in which case, possibly homoplasious).

Thus there appears to be a degree of uncertainty associated with some portions of the stronger of the two cladograms (Fig. 3). However, the cladogram in Fig. 3 is more parsimonious, and also more clearly resolves the species of subg. Heterocharis as the most primitive in Eucharis. Though it is undoubtedly a controversial decision from an orthodox cladistic perspective, I prefer to recognize Urceolina and Caliphruria as distinct genera, despite the attendant risk of a

paraphyletic Eucharis. The ancestral node in Fig. 3 from which Urceolina, Caliphruria, and Eucharis subg. Eucharis forms a monophyletic group is defined by only 2 apomorphies (reversals to numerous flowers and short staminal teeth). Thus, this monophyletic group is not very well supported.

Ashlock (1979) presents a very eloquent argument for acceptance of paraphyletic groups. Ashlock argues that an evolutionary systematic approach to a group of organisms should equally reflect anagenesis [degree of divergence (= number of apomorphies)] as well as cladogenesis. He defines two subclasses of monophyletic groups: holophyletic, which contain all descendents of the stem ancestor, and paraphyletic, those which do not. Ashlock claims that orthodox cladists, by ignoring the anagenetic aspect of evolution (i.e., basing their classifications strictly on branching pattern), reduce the information content of their classification.

In the first cladogram (Fig. 3), Urceolina and Caliphruria are defined by 9 and 12 apomorphies respectively. The stem HTU (hypothetical taxonomic unit) of subgenus Eucharis is defined by six apomorphies, two of which (well-developed and shallowly cleft staminal cup) are probably false, as they more than likely represent retention of the ancestral state. Three of the remaining four are all androecial characters, an area of extensive morphological plasticity throughout the pancratioid Amaryllidaceae. Thus, the only major apomorphy separating subg. Eucharis from all other taxa in this clade is the orange, mimetic capsule.

In terms of patristic distance, Eucharis is much closer to the three species of subg. Heterocharis than either Caliphruria or

Urceolina. In the generalized sense, the distribution of subg. Heterocharis is quite broad, from Colombia to Peru (Fig. 2). However, each of the three species of subg. Heterocharis itself are only narrowly distributed. Eucharis sanderi is known only from the Chocó region of Colombia. Eucharis amazonica is found natively only in the middle Río Huallaga valley of Peru. Eucharis anomala, cladistically the most ancestral species in the genus (Fig. 3), has been collected outside of Ecuador only once. More significantly, E. anomala is the only species of Eucharis found on both sides of the Andes. I believe that all three species of subg. Heterocharis represent the relictual remnants of the ancestral eucharoid complex, each of which has remained isolated long enough to evolve its respective cohort of autapomorphies.

Eucharis oxyandra is a taxonomically perplexing species in its characters of morphological intermediacy between Eucharis and Urceolina. It is known only from bulbs found in local, transient cultivation in Peru, near the single recorded point of geographic sympatry between Eucharis (E. amazonica) and Urceolina (U. microcrater). The absence of data on fruit and seed morphology of this species further occludes resolution of its phylogeny. Eucharis lehmanni presents a similar problem.

It is unfortunate that Traub (1971) never saw fit to supply supporting data for his broad concept of Eucharis, Caliphruria and Urceolina as a single, polymorphic genus. It is a cladistically justifiable concept.

Equally sound cladistically is the recognition of Eucharis, Heterocharis, Caliphruria and Urceolina as distinct genera. From a practical standpoint, I find this unsatisfactory, due to the close

phenetic relationship between subg. Heterocharis and Eucharis. This relationship is most conspicuous if one compares Eucharis bakeriana and E. formosa (the most primitive species of subg. Eucharis) with E. amazonica and E. anomala (subg. Heterocharis).

Alternatively, Urceolina and Caliphruria could be treated as two subgenera of Urceolina according to the cladogram in Fig. 3, if their sister group relationship is deemed accurate. This relationship is, however, arguable. In the context of pancratioid evolution in Amaryllidaceae (Meerow, 1985, 1987; Meerow and Dehgan, 1985), and modern concepts of familial limits in monocots (Huber, 1969; Dahlgren et al., 1985), I propose recognition of Eucharis, Caliphruria and Urceolina as distinct genera, with the acceptance of paraphyly in Eucharis. Until further data allows a more accurate understanding of their relationships, I also prefer to maintain E. lehmannii and E. oxyandra as species of Eucharis, with the notation incertae sedis.

In three neotropical lineages of the Pancratioidinae, parallel trends in the evolution of floral morphology have occurred (Meerow, 1985). In each case, taxa with smaller, tubular or ventricose, brightly colored flowers with reduced staminal connation, and without noticeable fragrance have diverged from taxa possessing a large, white, fragrant, crateriform flower with a staminal cup (Meerow, 1985). The pancratioid flower correlates repeatedly with the largest pollen grain size within the subfamily (Meerow, 1985; Meerow and Dehgan, 1985). Presumed basal complexes within each pancratioid lineage also have numerous ovules per locule, a character state considered primitive in the Amaryllidaceae (Traub, 1963). Eucharis and Urceolina, as documented in this paper, present one such case. Pseudostenomesson Velarde, perhaps prematurely

submerged by Traub (1980) as section Artema of Hymenocallis on the basis of leaf and seed morphology, presents a parallel situation within the Hymenocallis lineage (Meerow, 1985; Meerow and Dehgan, 1985). Tribe Stenomesseae contains two small, genera, Pamianthe and Paramongaia, with ancestral floral morphology, and a large genus, Stenomesson, with derived morphology. Each lineage appears to be a monophyletic group on the basis of vegetative and ovarian morphology, as well as chromosome number (Meerow, 1985, 1987; Traub, 1963). A similar pattern occurs in all three lineages: 1) floral morphology of "derived" taxa suggests an ornithophilous pollination syndrome and 2) "derived" taxa are found, entirely or in part, at higher elevations than presumed ancestral taxa. In the Hymenocallis and Eucharis lineages, the pancratioid floral morphology has radiated to a far greater extent than the putatively ornithophilous divergence (Pseudostenomesson and Urceolina, respectively). In the Pamianthe-Paramongaia/ Stenomesson lineage, it is the derived genus, Stenomesson (35-40 species), which has speciated to a greater degree than taxa with the ancestral pancratioid flower (Pamianthe: 3 species, Paramongaia: monotypic).

A pattern unique to the neotropical Pancratioidinae is the existence in modern times of small or monotypic genera with characters of intermediacy between more widely distributed genera. A number of these are known only from the type collections. Plagiolirion Baker and Matueua Klotzsch are two such taxa that Traub (1951) first merged with Eucharis, and later with Urceolina (Traub, 1971). However, from available data their affinities appear to be with Hymenocallis and Stenomesson respectively (Meerow, MS in subm.). Eucharis lehmannii and E. oxyandra may represent two such taxa within the eucharoid phylogeny.



There are only four recognized, Paleotropical pancratioid genera. Pancratium, ca. 17 species, is widely distributed from Africa, Mediterranean Europe, to Asia. The genus is badly in need of revision. Asian species are particularly poorly known. The relationship of Vagaría, (ca. 2 species) to Pancratium, is similar to that of Caliphruria and Eucharis. Divergence is concentrated in androecial characters. Eurycles (2 species) and Calostemma (2 species) are two Australasian genera, very different in leaf and floral morphology, but linked by the synapomorphy of a unique bulbiform seed (see Chapter IV). Pancratium and Vagaría have 22 chromosomes (Ponnamma, 1978; Meerow, unpubl. data); Eurycles and Calostemma have 20 (Zaman and Chakraborty, 1974; Meerow, unpubl. data). Neotropical taxa characteristically have 46 chromosomes (Di Fulvio, 1972; Flory, 1977; Meerow, 1984, 1985, 1987).

The much higher level of divergence in neotropical pancratioid lineages may thus be primarily a factor of two causes, 1) the uplift of the Andes, creating much opportunity for geographic isolation, and 2) greater genetic adaptability, via tetraploidy, to new ecological zones.

Northern South America has had a tropical climate since the Cretaceous (110 Ma; Darlington, 1965). After the initial appearance of the pancratioid complex, the eucharoid line probably diverged from other pancratioid lineages, perhaps becoming well represented in the rainforest understory across northern South America. Uplift of the Andean geosyncline prior to the Pliocene (10 Ma) was not pronounced (Van der Hammen, 1974). At the beginning of the Pliocene, the present-day high plane of Bogotá, Colombia remained in the tropical belt (Van der Hammen, 1979). During the Pliocene, massive uplift of the Andean



cordillera close to present elevational limit occurred (Van der Hammen, 1979). Eucharis, as presently circumscribed, is rarely found indigenous at elevations above 1000 m. If such a proto-eucharoid complex was found across the northern South American tropical belt, expressing the same fidelity to mesic, lowland sites as extant taxa, uplift of the Andes would effectively have splintered populations of this complex into several sets of populations. These would then have been separated by the parallel chains of the Andes and their intervening high valleys, plateaus, and xeric lowland valleys, formidable dispersal barriers to organisms adaptively linked to lowland rainforest ecology. Massive extinction of intervening populations probably occurred. Subsequent to the Andean uplift, taxa of the eucharoid line would have been restricted to two geographical areas: 1) premontane rainforests of the Pacific slope of the northern Andes and 2) the corresponding habitat on the eastern slopes of the Amazonian drainage. It is within these areas that the greatest diversity of these taxa is concentrated. The continuous uplift of the Andes, and Pleistocene refugia effects (see Chapter IX) has had further impact on the evolution of these groups. If the evolution of Caliphruria and Urceolina is as recent as this scenario might suggest, the occurrences of rare intergeneric hybridization in the wild may reflect large-scale morphological differentiation as a preface to large-scale genetic divergence. This is exactly what Davis and Gilmartin (1985) discuss in their review of morphological variation and speciation. Much broader based isozyme studies of these taxa than detailed in Chapter VIII are planned to address this issue in the Amaryllidaceae.

Huber (1969) revolutionized thought on monocot phylogeny by pointing out that monophyletic groups of genera could be resolved within traditionally broad family concepts of the Liliiflorae. Dahlgren and coworkers (e.g., Dahlgren and Clifford, 1982; Dahlgren et al. 1985) have adopted much of Huber's data into a phylogenetic classification of the monocots with much narrower family limits than previously proposed by modern taxonomists working above the family level. Dahlgren et al. (1985) have classified the petaloid monocots on the strict basis of apomorphies, rather than by overall similarity and, consequently, their many obvious symplesiomorphies.

Detailed study of Eucharis, Caliphruria, and Urceolina reveal that each has evolved its own complement of autapomorphic characters, some of which (e.g., multicellular stigmatic papillae in Caliphruria; mimetic capsule in Eucharis; unique seed morphology and anatomy in Urceolina) do not reoccur in the Amaryllidaceae. Rather than join these taxa on the basis of their obvious phenetic similarities, a consequence of their common ancestry, I prefer to recognize their diversity at the generic level, and their common ancestry at the tribal rank (= Euchareae).

Table 11.1. Characters, character states, and transformation series for cladistic analysis of Eucharis and Caliphruria. For simple two-state characters, the transformation is always A ---> B.

1. Leaves: A. linear or lorate, sessile; B. petiolate. 2. Leaves: A. deciduous; B. deciduous and hysteranthous; C. persistent; A ---> B, A ---> C. 3. Leaves: A. plicate; B. smooth. 4. Leaf margins: A. non-undulate; B. undulate. 5. Petiolar secondary bundles: A. absent; B. present. 6. Abaxial cuticular striations: A. absent or nearly so; B. dense, well-developed. 7. Epidermal cell anticlinal walls: A. more or less straight; B. undulate. 8. Flowers: A. more than 7 cm long; B. 5-7 cm long; C. less than 5 cm long; A ---> B ---> C. 9. Floral fragrance: A. heavy; B. mild; C. absent; A ---> B ---> C. 10. Flower number: A. more than 5; B. ca. 5; C. less than 5; A ---> B ---> C. 11. Flower color: A. white; B. white or yellow; C. yellow or orange; A ---> B, A ---> C. 12. Flower habit: A. erect or sub-erect; B. declinate or pendent by curving of tube; C. declinate or pendent by laxness of pedicel; A ---> B, A ---> C. 13. Pedicel length: A. flower (sub)sessile; B. less than 0.5 cm; C. greater than 0.5 cm long; A ---> B ---> C. 14. Tube habit: A. straight; B. curved. 15. Tube length: A. longer than tepals; B. equal to or shorter than tepals. 16. Tube color: A. green; B. concolorous with tepals. 17. Tube morphology: A. cylindrical proximally, dilating at 1/2 to 1/3 of its length; B. funnellform, dilating gradually from the base; C. cylindrical for most of its length, dilating abruptly near the throat; A ---> B; A ---> C. 18. Perianth morphology: A. crateriform; B. campanulate; C. funnellform; D. urecolate; A ---> B, A ---> C, A ---> D. 19. Staminal cup: A. well-developed; B. reduced. 20. Androecial pigmentation: A. primarily on interior of cup; B. equally on interior and exterior; C. absent; A --->

Table 11.1--continued.

B, A ---> C. 21. Staminal cup: A. non-plicate; B. plicate; C. reduced; A ---> B, A ---> C. 22. Staminal cup: A. shallowly cleft between stamens (< 2 mm); B. deeply cleft (> 2 mm); C. reduced; A ---> B; A ---> C. 23. Free filament: A. linear (< 1 mm wide); B. subulate (> 1 mm wide). 24. Staminal dentation: A. present; B. polymorphic; C. absent. A ---> B, A ---> C. 25. Staminal teeth: A. shorter than free filament; B. more or less equal to free filament; C. longer than free filament; D. absent; A ---> B ---> C, A ---> D. 26. Anthers: A. versatile at anthesis; B. erect at anthesis. 27. Pollen longest equatorial diameter: A. greater than 80  $\mu$ m; B. 76-80  $\mu$ m; C. 66-75  $\mu$ m; D. 60-65  $\mu$ m; E. 50-59  $\mu$ m; A ---> B ---> C ---> D ---> E. 28. Pollen exine reticulation: A. coarse; B. moderately coarse; C. fine; A ---> B ---> C. 29. Style exserted: A. greater than 1 cm beyond anthers; B. 1 cm or less beyond anthers, but above the rim of the staminal cup; C. to or below the rim of the staminal cup; A ---> B ---> C. 30. Stigma: A. trilobed; B. capitate, entire. 31. Stigmatic papillae: A. unicellular; B. multicellular. 32. Ovary color: A. green; B. white. 33. Ovary: A. rostellate; B. not rostellate. 34. Ovule number (per locule): A. 10-20; B. 7-10; C. 3-6; D. 2-3; A ---> B ---> C ---> D. 35. Ripe capsule: A. green, relatively thin-walled; B. leathery, orange. 36. Seeds: A. compressed; B. globose or ellipsoid; C. narrowly oblong, curved; A ---> B; A ---> C. 37. Testa: A. black; B. blue; C. brown; A ---> B; A ---> C. 38. Testa: A. dull; B. lustrous. 39. Testa: A. smooth; B. rugose. 40. Somatic chromosome number: A. 22; B. 34; C. 46; D. 68; E. 92; A ---> B ---> C ---> D, C ---> E.

Table 11.2. List of OTU's and label designations for cladistic analysis of Eucharis and Caliphruria. \* = outgroup.

TAXON	DESIGNATION
<u>Eucharis amazonica</u>	AMA
<u>E. anomala</u>	ANO
<u>E. astrophiala</u>	AST
<u>E. bakeriana</u>	BAK
<u>E. bonplandii</u>	BON
<u>E. bouchei</u>	BOU
<u>E. candida</u>	CAN
<u>E. castelnaeana</u>	CAS
<u>E. corynandra</u>	COR
<u>E. cyaneosperma</u>	CYA
<u>E. formosa</u>	FOR
<u>E. plicata</u> subsp. <u>plicata</u>	PLI-P
<u>E. formosa</u> subsp. <u>brevidentata</u>	PLI-B
<u>E. lehmannii</u>	LEH
<u>E. oxyandra</u>	OXY
<u>E. sanderi</u>	SAN
<u>E. ulei</u>	ULE
<u>Caliphruria hartwegiana</u>	HAR
<u>C. korsakoffii</u>	KOR
<u>C. subdentata</u>	SUB
<u>C. tenera</u>	TEN

Table 11.2--continued.

TAXON	DESIGNATION
* PANCRACTIUM	PAN
URCEOLINA	URC
* LEPIDUCHITON ( <u>Hymenocallis</u> <u>quitoensis</u> & <u>H. heliantha</u> )	LEP
ANCESTOR	ANC



Table 11.3. Character state matrix for cladistic analysis of Eucharis and Caliphruria. Refer to Table 11.2 for key to OTU abbreviations. No value indicates unknown character state.

[illegible]

Figure 11.1. Character states of *Urceolina*. All photos are *U. microcrater* Kränzl. (Schunke 13633, FLAS), unless otherwise stated. A. Flowers (Plowman & Kennedy 5721, GH). Photo courtesy T. Plowman. B-C. Epidermal cell configurations. B. Abaxial. C. Adaxial. Scales = 0.1 mm. D. SEM photomicrograph of abaxial leaf surface. Scale = 25  $\mu$ m. E. SEM photomicrograph of *U. urceolata* pollen grain (Weberbauer 7822, US), proximal polar view. Scale = 5  $\mu$ m. F. Ovary. G. SEM photomicrograph of stigma. Scale = 50  $\mu$ m. H. Seed. I-L. Longitudinal transverse sections of seed. I. Micropylar end of seed. J. Chalazal end of seed. K. Apex of embryo. Scale = 100  $\mu$ m. Internal chalazal "cap". Scale = 200  $\mu$ m. em = embryo, en = endosperm, t = testa, c = cap.

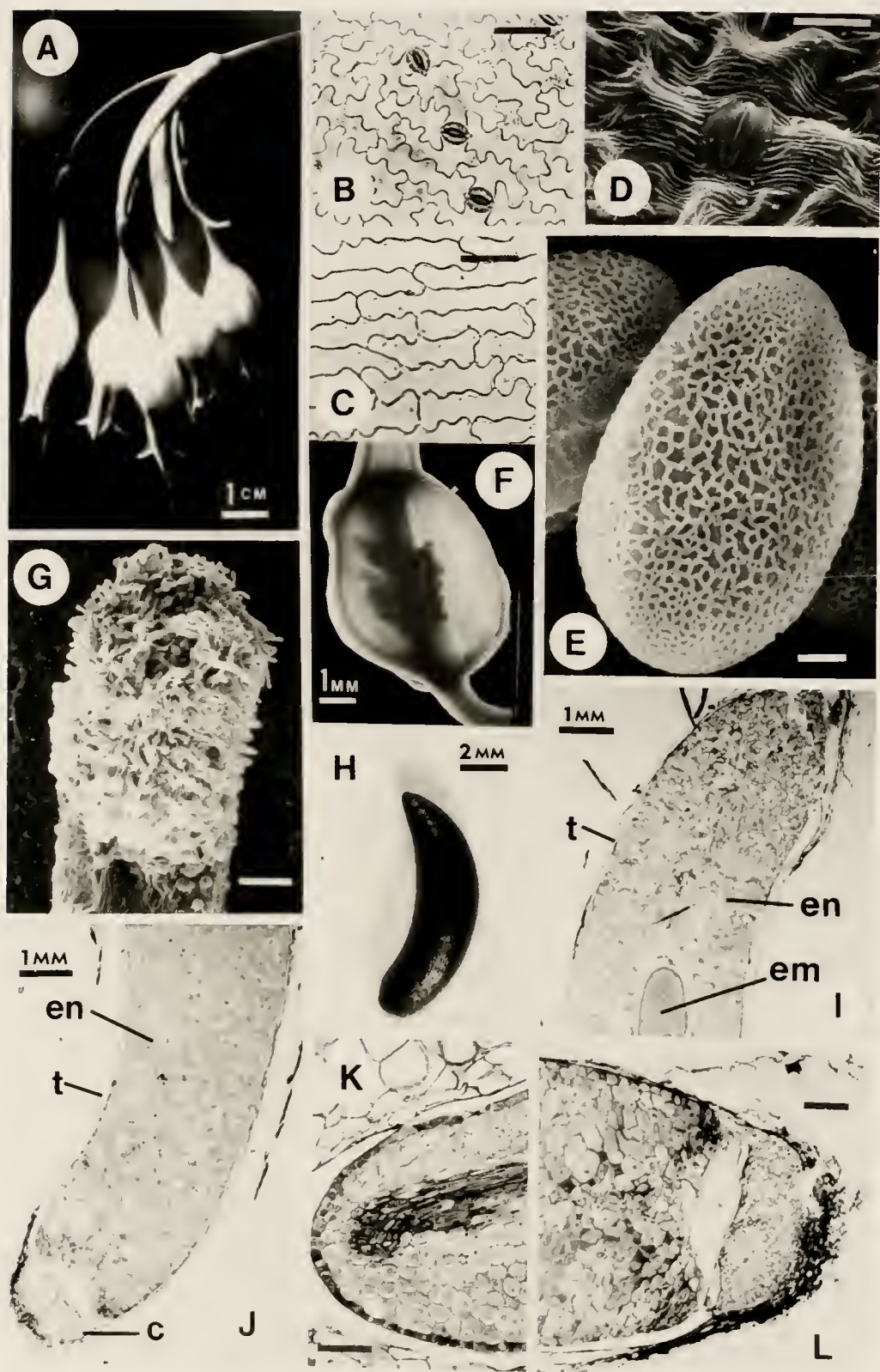


Figure 11.2. Generalized distributions of Eucharis, Caliphruria and Urceolina in Central and South America.



Figure 11.3. Cladogram of Eucharis and Caliphruria, based on data matrix in Table 3. Broken line indicates zero-length branch.



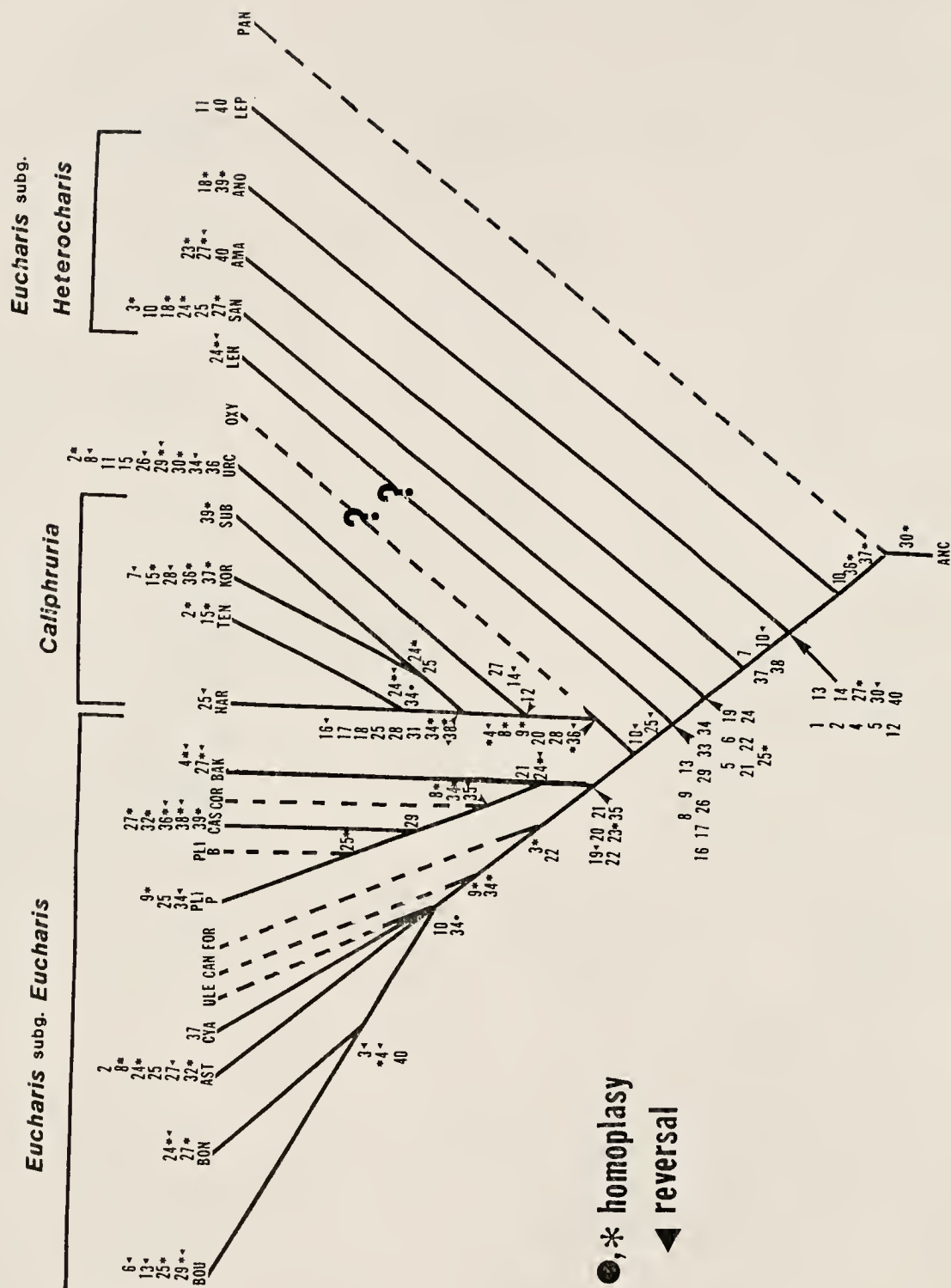
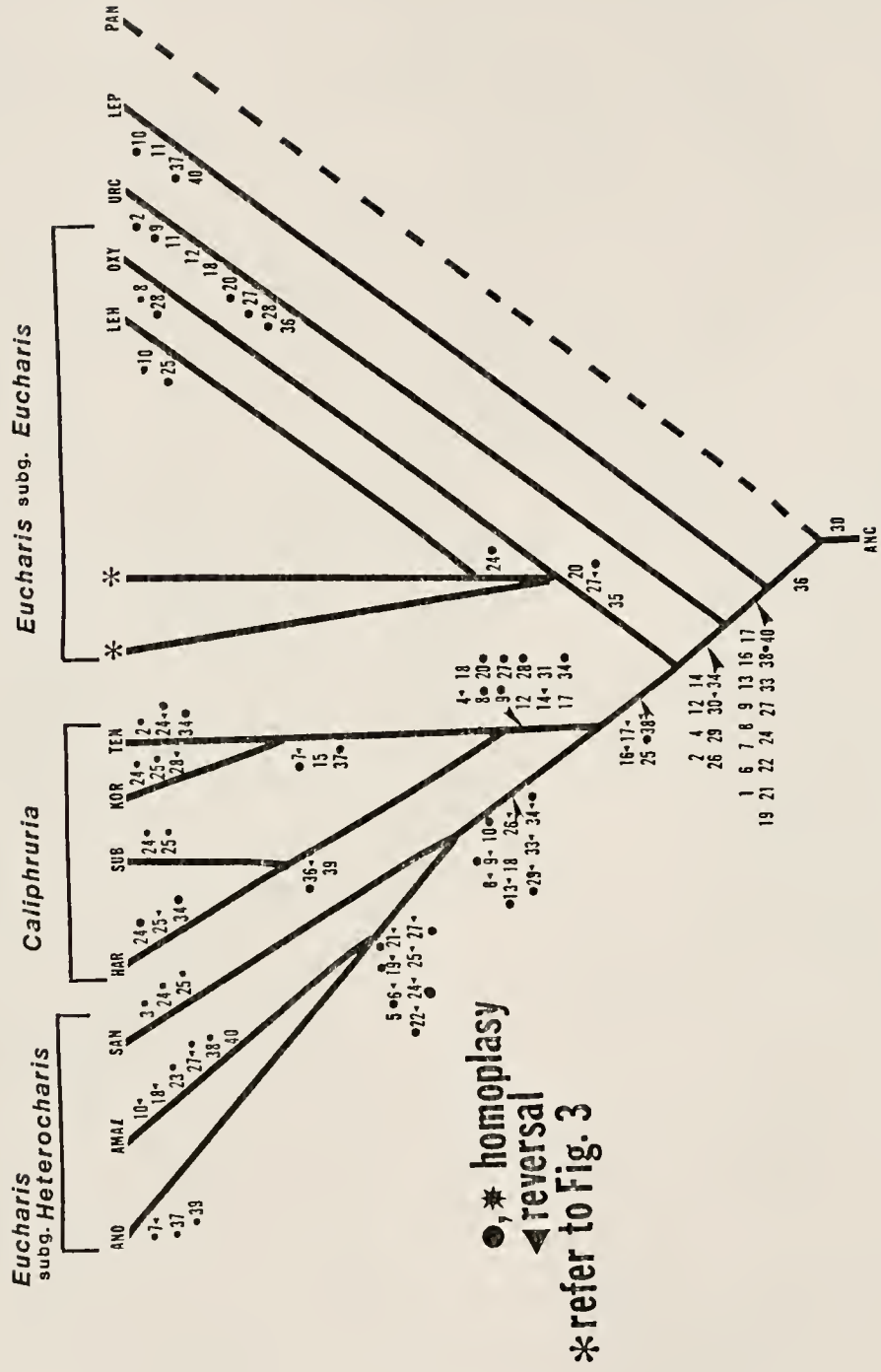


Figure 11.4. User-generated cladogram of Eucharis, Caliphruria, and Urceolina. Broken line indicates zero-length branch.



## CHAPTER XII TAXONOMIC TREATMENT

### Materials and Methods

#### Herbarium Studies

Loans or gifts of herbarium specimens were received from the following herbaria: AAU, B, BM, COL, F, FTG, G, GB, GH, GOET, HUNT, K, LE, M, MG, MICH, MO, MPU, NA, NY, OXF, P, QCA, S, SEL, SP, U, UC, US, VEN.

#### Living Collections

Over 100 accessions of living material representing 15 species or natural hybrids of Eucharis and Caliphruria were accumulated from personal field collections and from the following individuals or institutions: James Bauml, Libby Besse, Calaway Dodson, Robert Dressler, Mark Elliot, Thomas Fennell, Fred Fuchs, Harry Luther, Fred Meyer, Timothy Plowman, James Watson, Mark Whitten, Margot Williams, Norris Williams, Marcia Wilson, Bailey Hortorium, Royal Botanic Gardens at Kew and Edinburgh, Longwood Gardens, UC Berkeley Botanical Garden, Honolulu Botanical Gardens, Huntington Botanical Garden, Fairchild Tropical Garden, Marie Selby Botanical Garden, Missouri Botanical Garden, and Strybing Arboretum. Voucher specimens for living material utilized in the various systematic investigations enumerated in previous chapters are deposited at FLAS.

### Field Studies

Field work was conducted in Peru and Ecuador in July-August, 1982, and in Colombia and Ecuador in July-August, 1984. Herbarium specimens and living material were collected, and ecological observations of natural populations were made.

### Notes on Critical Measurements

Measurements of vegetative and floral parts in the following species descriptions are derived from examination of dried material (floral parts after rehydration in a 3% solution of Aerosol OT brought to boil), supplemented with examination of fresh or FAA-preserved material when available. In all cases where dried and fresh or spirit preserved material of the same collection was available, I found less than 5% difference between measurements of rehydrated and fresh or preserved tissue.

Measurements of the staminal cup are frequently critical in delimiting taxa of Eucharis possessing a well-developed cup, and the criteria used in assessing size of the androecium requires special consideration. Length measurements of the staminal cup were made from the base to the apex of the teeth or lobes of the cup, not including the subulate portion of the filament. In only two cases (E. astrophiala and E. bouchei var. bouchei), where each stamen dilates gradually from apex to base in all or some populations, do length measurements refer to the entire length of the androecium. The width of the staminal cup, where relevant, was measured at the rim of the cup in those species where the stamens constrict distally into a narrow, subulate portion; and at the widest point along the stamens in those taxa in which the stamens dilate

gradually from apex to base. These measurements are graphically illustrated in Figure 1.

#### A Note on the Keys

Taxa of Caliphruria and E. subg. Heterocharis are separable by discrete characters or character states very amenable to key construction. Using the keys to these two subgenera, any worker should be able to identify material referable to described taxa of either group, whether in the field or in the herbarium. The enormous degree of phenotypic plasticity exhibited by species of subg. Eucharis, however, made key construction difficult. Most species of subg. Eucharis overlap to at least some degree with one or more other species in virtually all quantitative morphological characters. As a consequence, major dichotomies in the key to subg. Eucharis are not as discrete as one would prefer. In some cases, I have had to rely on characters observable only with living material. With perserverance, any worker should be able to key out all but the most depauperate herbarium specimens of subg. Eucharis.

#### Species Concept

The great degree of morphological variation demonstrated by many species of E. subg. Eucharis renders a purely taxonomic species concept unworkable. Narrow concepts of morphological species in this genus, have little biological basis, and would result in an enormous increase in the number of recognized species.

Mayr (1969, p. 26) defined the biological species as "groups of interbreeding natural populations that are reproductively isolated from



other such groups." At present, there is insufficient data concerning population dynamics and breeding behavior of Eucharis and Caliphruria to support an exclusively biological species concept in this genus. In at least one case (E. plicata and E. ulei), interspecific hybridization and perhaps introgression between two species has occurred. In addition, I recognize several other putative natural interspecific hybrids in Eucharis, and one inter-generic hybrid (X Calicharis butcheri). The evidence from artificial hybridization attempts suggests that a number of species of E. subg. Eucharis are cross-compatible, though most natural hybrids show reduced pollen stainability.

The evolutionary species concept of Simpson (1961) and Wiley (1978, 1981) is defined as "a lineage of ancestor-descendent populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate" (Wiley, 1981, p. 25). Though reproductive isolation may be necessary to maintain the integrity of an evolutionary species, its identity, as defined by morphological similarity, is conceived as the result of the common ancestry of its component populations. I have striven in my work on Eucharis and Caliphruria to adhere to an evolutionary species concept, using as broad a morphological data base as possible, and subjecting the data to both phenetic and phylogenetic analyses. Insights from chromosome cytology and analyses of genetic variation have at times provided additional support for species delimitation.

The rank of subspecies is used once in this treatment (E. plicata) to designate strong morphological divergence coupled with geographical isolation which, in my opinion, is acceptable within the confines of specific limits. The rank of variety is used in a case (E. bouchei)

where both the morphological and geographic components of divergence are weaker, but appear to represent the first stages of speciation within a heterozygous semi-species complex (Grant, 1981).

### Taxonomic Treatment

#### Key to Eucharis and Caliphruria:

1. Leaf margins usually undulate; flowers declinate to pendulous via the curving of the tube; perianth funnelform-campanulate or crateriform; tube cylindrical, at least below middle, abruptly dilating at or above the midpoint of its length, curved, 25-50 mm long; staminal cup conspicuous, basally pigmented green or yellow, exserted from the throat of the perianth or adnate to the dilated portion of the tube; stigmatic papillae unicellular ..... Eucharis
1. Leaf margins non-undulate; flowers declinate to sub-pendulous via the curving of the pedicel; perianth funnelform; tube funnelform, dilating gradually from base (rarely sub-cylindrical), straight or only slightly cernuous, 25 mm or less long; staminal cup inconspicuous and unpigmented, reduced to a membranous, basal connation of the filaments; stigmatic papillae multicellular ..... Caliphruria

EUCCHARIS Planchon. Linden's Ann. Cat. Hort. 8: 3. 1852; Fl. des Serres Ser. 1, 8: 107. 1853. TYPE SPECIES: Eucharis candida Planchon et Linden. Urecolina subg. Eucharis (Planchon) Traub. Pl. Life 27: 57-59. 1971.

Evergreen (one species ± deciduous), bulbous geophytes. Bulb tunicate, usually offsetting vigorously. Leaves petiolate, persistent, glabrous; petiole sub-terete, somewhat concave adaxially proximal to the

sinus, convex abaxially, light green, winged distally by the attenuation of the lamina; lamina ovate, elliptic, ovate- or elliptic-lanceolate, usually thin, predominately hypostomatic, usually lustrous, dark green adaxially, light or silvery green abaxially, smooth or plicate between the parallel veins, cuticle of the abaxial epidermis variably striate, margins frequently undulate, apically acute or acuminate, basally attenuate to the petiole, rarely appearing sub-cordate. Inflorescence scapose, umbellate (composed of 1 to several, reduced, helicoid cymes); scape solid, terete or slightly compressed, glaucous, terminating in two green or greenish-white, ovate-lanceolate, valvate-imbricate, marcescent bracts that enclose the flowers and several secondary bracts before anthesis. Flowers 2-10, pedicellate (rarely subsessile), each subtended by a lanceolate bracteole, pendent or declinate, sometimes fragrant, white, protandrous; perianth crateriform or campanulate; tube cylindrical, dilating abruptly above its midpoint, sometimes stained green proximally; limb of 6 tepals in 2 series spreading widely from the throat or imbricate for half their length, the outer series usually longer, narrower and apiculate; the inner series acute, obtuse, or minutely apiculate. Stamens 6, variously connate below, pigmented yellow or green proximally; free filament linear, subulate, or otherwise petaloid; anthers oblong to linear, sub-basifixed or dorsifixed, eventually becoming versatile, introrse, dehiscent longitudinally; pollen grain boat-shaped elliptic, monosulcate, exine reticulate. Style filiform, included within, equal to, or exserted from the staminal cup; stigma obtusely 3-lobed, glandular-papillose. Ovary inferior, green or white, globose-ellipsoid, oblong, occasionally trigonous, 3-locular; septal nectaries present; ovules 2-20 per locule, placentation axile,

globose, anatropous. Fruit a 3-lobed, loculicidal capsule, thin-walled or leathery, green or bright orange; seed globose or ellipsoid, sometimes angled by pressure, turgid, with copious endosperm, few per locule; testa thin, phytomelanous, lustrous (rarely dull) black, dark brown or blue, usually smooth.  $2n = 46, 68, 92$ .

Key to the subgenera of Eucharis:

1. Flowers 3 to 7 cm long, usually pendulous, only rarely and mildly fragrant, crateriform (rarely somewhat campanulate); perianth tube cylindrical below, dilated abruptly just below throat, usually strongly curved, white; limb usually segments spreading widely (ca. 90°) at perianth throat; staminal cup inserted at throat of tube, proximally spotted or stained yellow, green or yellow-orange equally on the exterior and interior of the cup; distal part of filament usually widely subulate (> 1.5 mm wide) or otherwise petaloid; anthers more or less erect at anthesis; ovules 2-9 (-10) per locule ...  
 ..... subg. Eucharis
1. Flowers 7-8 cm long, declinate or sub-pendulous, strongly fragrant, funnelform-campanulate to crateriform; perianth tube cylindrical below, abruptly dilated at 1/3-1/2 its length, green (at least proximally); limb segments usually imbricate for half their length; staminal cup partially adnate to upper portion of tube, sometimes reduced, flushed (yellow-)green, particularly along the filamental traces, with the pigmentation most intense on the interior of the cup; distal portion of the filament usually narrowly subulate

(1 mm or less wide); anthers versatile at anthesis; ovules

(7, 9-) 16-20 per locule ..... subg. Heterocharis

EUCHARIS subg. EUCHARIS.

Leaves glabrous, petiolate, persistent; lamina ovate, elliptic or lanceolate, mostly thin, margins usually undulate, variably plicate between the parallel veins, apically acute or acuminate, basally attenuate to the petiole or rarely subcordate, mostly dark green and lustrous adaxially, light or silvery-green abaxially, the abaxial epidermis variously striate; petiole subterete, somewhat channelled adaxially proximal to the sinus. Inflorescence scapose, umbellate, terminating in two greenish-white marcescent bracts. Flowers pedicellate, (3-) 5-10, only rarely with noticeable fragrance, mostly pendulous, 3-7 cm long, crateriform (rarely slightly campanulate); perianth tube usually strongly curved, cylindrical below, dilated just below the throat or rarely at 1/3 length, white; limb of six white, ovate to ovate-lanceolate tepals which usually spread widely from the throat, often recurved above the middle, the outer three usually longer, narrower and apically apiculate, the midvein often faintly yellow in strong light. Stamens connate into a conspicuous staminal cup, usually exserted from the rim of the throat, cup rarely reduced; staminal cup apically white, marked green or yellow (rarely yellow-orange) basally, variously toothed, lobed or entire; distal portion of the filaments petaloid and variously shaped; anthers oblong or linear, sub-dorsifixed or sub-basifixed, more or less erect at anthesis, finally becoming versatile; pollen grain 45-60  $\mu\text{m}$  (polar axis), 55-86  $\mu\text{m}$  (longest equatorial axis), the exine coarsely reticulate. Style filiform, white; stigma obtusely trilobed, glandular pubescent. Ovary globose, elliptic



or trigonous, green or white; ovules globose to ellipsoid, axile, superposed, 1-12 per locule, most often 2-4. Fruit a loculicidal capsule, orange and leathery when ripe (rarely remaining green); seeds 1-3 (-4) per locule, ca. 1 cm long, turgid, ellipsoid (rarely somewhat compressed), with a lustrous black or blue testa. 13 species, (Guatemala) Costa Rica to Bolivia, concentrated on the lower slopes of the northeastern Andes and in lowland Amazonas.

Key to the species of subg. Eucharis:

1. Perianth tube 25 mm or more long.
  2. Flowers (7-) 8-10 (very rarely 5), ovules 3-9 per locule (very rarely 2).
    3. Flowers not fragrant; perianth tube (25-) 30-35 mm long; outer tepals (20-) 25-30 (-33) mm long; staminal cup 8-11 mm long to apex of teeth or lobes; ovules (2-) 3-5 (-7) per locule ..... 1. E. candida
    3. Flowers mildly fragrant; perianth tube 35-45 (-50) mm long; outer tepals (28-) 32-45 (-47) mm long; staminal cup 10-16 mm long to apex of teeth or lobes; ovules (2-4) 7-9 per locule.
    4. Floral fragrance slightly fetid; flowers pendent; staminal cup less than 15 mm long to apex of teeth or lobes, cleft between each stamen 3-5 mm long, non-plicate; staminal teeth, if present, much less than half the length of the subulate portion of the filament; style exerted ca. 1 cm beyond the anthers ..... 2. E. formosa



4. Floral fragrance sweet; flower perpendicular to vertical axis of scape; staminal cup more than 15 mm long to apex of teeth, cleft very shallowly (less than 2 mm) between each stamen, plicate; staminal teeth half the length of the subulate portion of the filament; style exerted less than 0.5 cm beyond the anthers ..... 3. E. bakeriana
2. Flowers 3-5 (-7); ovules 2-3 (-5) per locule.
5. Leaves non-plicate, somewhat succulent, margins non-undulate, length : width ratio usually less than 3; petiole usually shorter than the lamina; plants of central and western Colombia or Central America.
6. Leaves slightly glaucous adaxially; abaxial cuticle densely striate; perianth tube 25-33 mm long; staminal cup irregularly toothed, proximally pigmented pale yellow; stamens always constricted distally into a narrow subulate portion; style exerted less than 0.5 cm beyond anthers; ovary not trigonous; plants of Colombia ... 4. E. bonplandii
6. Leaves not glaucous, abaxial cuticle largely devoid of striations; perianth tube (25-) 33-45 mm long; staminal cup most frequently edentate, proximally pigmented green; stamens often dilating gradually from apex to base; style exerted 0.5-1 cm beyond anthers; ovary often trigonous; plants of Central America ..... 5. E. bouchei

5. Leaves plicate, thin, margins undulate, lamina length : width ratio usually greater than 3; petiole usually equal to or exceeding the lamina in length; plants of western Ecuador and Amazonas.
7. Leaves bullate-pustulate in texture, non-lustrous; staminal cup always edentate, pigmented yellow-orange proximally, cleft between each stamen to at least half its length; stamens deltoid, dilating gradually from apex to base; ovary white; plants of western Ecuador ..... 6. E. astrophiala
7. Leaves not bullate-pustulate in texture, lustrous; staminal cup usually bidentate or quadrate, pigmented yellow or green, cleft between each stamen for ca. 2-3 mm; stamens not deltoid, constricted distally into a narrow (less than 2 mm wide) subulate portion; ovary green; plants of Amazonas.
8. Perianth tube curved gradually throughout the proximal half; staminal cup spotted green in the proximal half of each stamen, usually bidentate but sometimes obtusely lobed (rarely one to several stamens quadrate); testa lustrous black ..... 7. E. ulei
8. Perianth tube usually curved abruptly above the ovary, then more or less straight for the rest of its length; staminal cup pigmented yellow proximally, usually quadrately lobed, but one

or several stamens occasionally toothed; testa

lustrous blue ..... 8. E. cyaneosperma

1. Perianth tube equal to or less than 25 (very rarely to 30) mm long.

9. Staminal cup usually less than 1 cm long to apex of teeth or lobes, but connate portion of filaments always much shorter than free, subulate portion.

10. Teeth of the staminal cup acutely long-lanceolate, equaling the subulate portion of the filament in length; ovules 10 per locule, plants of western Colombia ..... 9. E. lehmannii

10. Teeth of the staminal cup (when present) obtuse, much shorter than the subulate portion of the filaments; ovules less than 10 per locule; plants of Amazonas.

11. Perianth + campanulate; staminal cup reduced to a basal connation of the filaments 0.8-1.5 mm long, edentate or obtusely bidentate; free filaments narrowly subulate, ca. 1 mm wide; ovules 6-8 per locule ..... 10. E. oxyandra

11. Perianth crateriform, staminal cup 3.5 mm long (to apex of teeth), obtusely bidentate between each stamen; free filaments club-shaped (appearing elliptic-lanceolate in dried material), 1.8-2 mm wide, ovules 4-6 per locule ..... 11. E. corynandra

9. Staminal cup usually greater than 1 cm long to apex of teeth or lobes, but connate portion of filaments always longer than the free, subulate portion.

12. Leaves 7-12 (-14) cm wide; staminal cup campanulate, gradually dilating distally; plicate along the filamental traces; ovary green; capsule leathery, bright orange, dehiscent; seeds ellipsoid, with a lustrous, smooth black testa ..... 12. E. plicata
12. Leaves 3-6 cm wide; staminal cup funnelform-cylindrical to cylindrical, often abruptly dilated distally at 1/2-2/3 length, plicate between the filamental traces; ovary whitish; capsule green, thin-walled, often tardily dehiscent; seeds wedge-shaped, with a dull, rugose black testa ..... 13. E. castelnaeana

1. EUCHARIS CANDIDA Planchon et Linden (Figs. 2-4A). Linden's Ann. Cat. Hort. 8:3, 1852; Fl. des Serres Jard. Eur. Ser 1, 8: 107, 1853. TYPE: ex hort Linden, supposedly imported from Colombia, no other data, Planchon s.n. (MPU!). Urceolina candida (Planch. & Lind.) Traub. Pl. Life 27: 57-59. 1971.

Plant to ca. 6 dm tall. Bulb sub-globose, 3-5 (-6) cm long, 3-4 (-5) cm diam, neck 1-2.5 (-4) cm long, 1-2.5 cm wide; tunics brown. Leaves 1-2, petiole (15-) 18-30 (-35) cm long, ca. 7 mm thick proximally, ca. 3-4 mm thick distally; lamina elliptic, (18-) 30-35 cm long, (7-) 8.5-11.5 (-12) cm wide; acuminate, deeply plicate, dark green but only slightly lustrous adaxially, light green abaxially, abaxial cuticle striate, margins coarsely undulate. Scape (4-) 5-6 dm tall, 8-10 mm diam proximally, 4-5 mm diam distally; bracts 25-45 (-50) mm long, ca. 5-6 mm wide, ovate-lanceolate. Flowers (7-) 8-10, rarely as few as 5, without noticeable fragrance; pedicels (9-) 15-20 (-35) mm long; tube (25-) 30-35 mm long, ca. 2 mm diam for most of its length, abruptly

dilated to (7-) 10 (-11.5) mm at the throat; limb spreading to 4.5-6 cm wide; tepals sometimes recurved distally, outer tepals (20-) 25-30 (-33) mm long, (9-) 10.5-14 (-15) mm wide, ovate-lanceolate, apiculate, the apiculum only slightly or obscurely tufted adaxially; inner series (20-) 22-28 (-32) mm long, (10-) 12-15 (-20) mm wide, ovate, acute to minutely apiculate. Staminal cup (Fig. 4A) funnelform-cylindrical to slightly campanulate, rarely widely ampliate distally, (7-) 8-11 mm long (to apex of teeth or lobes), (10-) 13-16 (-18) mm wide, most frequently edentate and lobed between each stamen, but at times bidentate or irregularly toothed, widely spotted green to greenish-yellow below each stamen; teeth, when present, 1-2 mm long, < 1 mm wide, acute or obtuse; cup cleft for (2.5-) 3-5 (-6) mm between each stamen; stamens (3.5-) 4.5-5.5 (-6) wide proximally; distal subulate portion (3.5-) 4.5-6 (-6.5) mm long, 1.5-2 mm wide at the base; anthers (3.5-) 4-5 (-6) mm long, oblong; pollen grain 46.8-50  $\mu\text{m}$  polar diam, 68.7-73  $\mu\text{m}$  longest equatorial diam. Style (38-) 45-55 mm long, exserted 0.5-1 cm beyond the anthers; stigma 2-3 mm wide. Ovary globose-ellipsoid, green, 5-7 (-8) mm long, 4-6 (-7) mm diam; ovules (2-) 3-5 (-7) per locule. Capsule (1.5-) 1.8-2.4 cm long, (2-) 2.5-2.9 cm wide; pedicel 2-4 cm long; seeds 1-2 (3) per locule, ellipsoid, ca. 1 cm long, ca. 0.5 cm diam, with a lustrous, smooth black testa.  $2n = 46$ .

**DISTRIBUTION AND ECOLOGY:** Understory of primary rain forest chiefly in the Oriente of Ecuador, particularly the Río Napo valley, occasional in north Peru and southeast Colombia (Figs. 5-6), (100-180) 240-550 (1000-1600) m; flowering at any time of the year, but most frequently in February-March and August.

ADDITIONAL MATERIAL EXAMINED: COLOMBIA. **Amazonas:** Puerto Nariño, 24 Jul 1965, Lozano et al. 594 (COL); Trapecio amazónica, Loretoyacu River, ca. 100 m, Oct 1946, Schultes & Black 8478 (US). **Meta:** Sabanas de San Juan de Arama, margen izquierda del Río Güejar, alrededores del aterrizaje "Los Micos," 500 m, 22 Jan 1951, Idrobo & Schultes 1208 (COL, GH, NY, US). ECUADOR. **Napo:** Tena, wet forest, 27 Sep 1939, Asplund 8853 (S); El Napo, 1931, Benoist 4717 (P); 70 km downstream from Coca at Anangu, 260 m, 8-11 Aug 1982, Besse et al. 1598 (SEL); Tena-Puyo road, 550 m, Aug 1982, Besse et al. 1643 (SEL); Coca-Lago Agrio road, 45 km north of Coca, Río Palanda Yacu, 7 Jun 1983, Bohlin & Bohlin 319 (GB); km 5, Cotunda-Coca, 1130 m, 19 Jun 1963, Dodson et al. 14095 (SEL); orilla izquierda del Río San Miguel, Puerto Nuevo, 26 Mar 1953, Gutierrez V. 2687 (COL); Santa Rosa at Río Napo, ca. 400 m, 29 Feb 1972, Harling 11090 (GB); Hacienda Cotapino (Concepción), 550 m, 19-20 Feb 1968, Harling et al. 7121 (FLAS, GB); lower Río Aguarico (above puesto militar Puerto Loja, 7 Mar 1968, Harling et al. 7400 (GB); Coca, potreros and rastros near the village along road to Lago Agrio, ca. 250 m, 2 Feb 1974, Harling & Andersson 11682 (GB); Cañon de los Monos, ca. 12 km north of Coca, 250 m, 4 Feb 1974, Harling & Andersson 11719, FLAS specimen (FLAS); Misahuallí at Río Napo, 28 Mar 1969, Holguier 925 (FLAS, GB); environs of Limoncocha, 240 m, Jun 1978, Madison et al. 5326 (F, SEL). **Pastaza:** Mera, forest on shore of Río Pastaza, ca. 1000 m, 30 Jan 1956, Asplund 19120 (S); Puyo-Arajuno Road, 1-5 km SW Diez ed Agosto, ca. 900 m, 4 Feb 1980, Harling & Andersson 16862 (GB); 68 km north of Puyo on road to Tena, along creek, ca. 500 m, 26 Jul 1982, flowered in cultivation, 15 Jan 1985, Meerow 1144 (FLAS). **Morona-Santiago:** Huamboya, 1500-1600 m, 15 Feb 1944, Acosta-Solis 7469 (F).



PERU. **Amazonas:** 400 m atrás de La Poza, Río Santiago, 180 m, 23 Aug 1979, Huashikat 164 (MO). **Loreto:** Maynas, Río Ampiyacu, Pebas and vicinity, approx.  $3^{\circ} 10' N$ ,  $71^{\circ} 49' W$ , behind Pebas on trail north of town, 10 April 1977, Plowman et al. 6724 (F); Maynas, Santa María de Nanay, Colonia San Fransisco de Indies Yaguas, 1.5 km del Fundo Balcon, Río Momen, 106-110 m, 15 Nov 1984, Schunke 14155-B (F, FLAS).

**Putative hybrids with E. formosa:** ECUADOR. **Napo:** km 23 Lago Agrio-Baeza road, 350 m, Jul 1982, Besse et al. 1558 (SEL); 35 km south of Río Aguarico, Lago Agrio-Coca road, Jul 1982, Besse et al. 1563 (SEL); Río Coca, 10 km upstream from ferry crossing, 250 m, 28 Nov 1983, Besse et al. 1949 (SEL).

Eucharis candida was originally described from cultivated material supposedly originating from Colombia, a country in which the species has actually been encountered only rarely. The species previously has been delimited by the absence of staminal dentation, however, this character varies considerably throughout the range of E. candida, as in the related species E. formosa and E. ulei.

Eucharis candida is most common throughout the upper Napo Valley in eastern Ecuador, and is very often geographically sympatric with the larger-flowered and more widely distributed E. formosa (Figs. 5-6). To date, no species of Eucharis other than these two have been collected north of the Pastaza valley in eastern Ecuador. On the basis of herbarium study alone, Ecuadorean populations of these two taxa form a mosaic that seemed taxonomically insoluble until living material of both species from several populations was collected and flowered. Principal component analysis (see Chapter VI) supports recognition of these taxa as distinct species, and also suggest that E. candida and E. formosa

have hybridized in at least one area of sympatry. Patterns of allozyme variation (see Chapter VIII) and karyotype analysis (Chapter VII) further support the separation of these two species. The species may be ecologically allopatric, however. Plants of E. candida which I collected in 1982 were growing along the bank of a small creek, just above the high water line. Populations of E. formosa were encountered in more upland sites. Nonetheless, in one instance two specimens (Harling & Andersson 11719), one each of the two species, were collected under the same number. Patterns of genetic variation (Chapter VIII) suggest a monophyletic origin for these species, possibly in the Pastaza valley. Both species have radiated outward, perhaps more than once.

I believe the unprecedented degree of sympatry between these two species in Ecuador is inextricably related to their use by Indian people of the Napo and Pastaza basins. The bulbs are not only mashed for poultices, a general use to which many South American amaryllids are applied, but Indian women reportedly collect the plants quite actively for reasons they would not disclose (N. Whitten, pers. comm.). Of course, aboriginal people are not without an aesthetic, and the species of Eucharis have a pleasing aspect when in flower. Cultivation for ornamental as well as medicinal and ceremonial uses cannot be discounted. Most local inhabitants whom I met while collecting Eucharis in the Oriente were readily familiar with the plants when shown photographs. It is thus more than likely that both species have been vectored about eastern Ecuador through human agency for years, if not centuries, perhaps even being transplanted from the wild into transient agricultural settlements. When these small gardens were abandoned after a few years, the bulbs probably recolonized locally. I am doubtful that

even botanically astute aboriginal people would differentiate between such similar species as E. candida and E. formosa, and plants from allopatric populations may have been collected indiscriminently and cultivated together. Successive patterns of fragmentation and coalescence of rainforest during the Pleistocene (reviewed by Prance, 1982a, b) may also have influenced distribution patterns of these two species (see Chapter IX).

Alternatively, E. candida and E. formosa may fit the semi-species model of Grant (1981), in which genetic barriers have not solidified between two morphologically distinct, sympatric races. Pollen of one putatively hybrid collection (Besse et al. 1558) stains 100% with Alexander's (1969) stain. In gross morphology, the flower of this collection resembles E. formosa, and thus may represent a genet at the low end of the floral size range for E. formosa, and not a hybrid between it and E. candida. Another hypothesis might be that E. candida and E. formosa represent the segregating phenotypes of a single, highly heterozygous species, a situation possibly existing in the E. bouchei complex of Central America. However, allozyme variation patterns (see Chapter VIII) suggest a fair degree of genetic divergence between E. candida and E. formosa, and I have decided to recognize these two, distinct, phenetic entities at the species level, with the understanding that their biological relationships may present more than meets the eye.

Eucharis candida may be separated from E. formosa by its smaller leaves and flowers, complete absence of fragrance (E. formosa produces a mild, "sour" odor), and generally fewer ovules per locule (though both species are quite variable in ovule number). Both species probably originated in the Napo-Pastaza drainage of Ecuador where present-day

populations are now concentrated. Eucharis formosa is slightly better represented in the Pastaza valley than E. candida.

Despite a formidable range of morphological variation in E. candida (Figs. 3-4A), I do not find any patterns that lend themselves to delimiting infra-specific taxonomic categories. Peruvian populations of E. candida are exceptionally variable in the shape of the staminal cup (Fig. 3), even among flowers of the same inflorescence. Such phenotypic plasticity is characteristic of Eucharis, and the bane of any purely alpha-taxonomic approach to the genus.

2. Eucharis formosa Meerow, sp. nov. (Figs. 2, 4B, 7).

E. candida Planchon et Linden primo adspectu maxime simile sed in omnes partes grandiores, floribus leniter fragrantibus, cupula staminea subcylindrica, et ovulis plerumque in quoque loculo plurimioribus; differt praecipue a E. bakeriana N. E. Brown cupula staminea angustiore inter stamina fissa profundius. TYPE: Ecuador, Morona-Santiago, Road Limón-Macas, ca. km 20 from Limón, primary rain forest and rastros, 700-900 m, 26 Mar 1974, Harling & Andersson 12915 (holotype: GB!; isotype: FLAS!).

Plant to 6-8 dm tall. Bulb sub-globose, 4-7 cm long, 3-5 cm diam, neck 2-5 cm long, ca. 1 cm thick, tunics brown. Leaves 1-2 (-3); petiole 25-38 (-42) cm long, 8.5-1 mm thick proximally, 5-6 mm thick distally; lamina elliptic, (21-) 30-45 (-52) cm long, (8-) 11-15 (-16) cm wide, usually conspicuously plicate, dark green and only slightly lustrous adaxially, light green abaxially, abaxial cuticle striate, margins coarsely undulate. Scape (5-) 6-7 (-8) dm tall, ca. 1 cm diam proximally, 5-6 mm diam distally; bracts ovate-lanceolate, (36-) 43-60 (-85) mm long, 10-15 cm wide at the base. Flowers 8-10, very rarely

less, pendent, emitting a mild, "sour" odor; pedicels (8-) 12-18 (-30) mm long; tube 35-45 (-50) mm long, ca. 2-2.5 mm wide for most of its length, abruptly dilated to (9-) 10-13 (-14) mm at the throat; limb spreading to (55-) 60-70 (-80) cm; tepals sometimes recurved distally; outer tepals narrowly ovate, (30-) 35-45 (-47) mm long, (10-) 15-18 (-20) mm wide, apiculate, apiculus conspicuously horned adaxially (Ecuadorean populations); inner tepals ovate, (28-) 31-40 (-45) mm long, (15-) 18-22 (-25) mm wide, acute to minutely apiculate. Staminal cup (Fig. 4B) funnellform-cylindrical, 10-13 (-15) mm long (to apex of teeth or lobes), (15-) 17-20 (-22) mm wide; flushed greenish-yellow proximally, with the greatest concentration of pigment below each free filament, rarely only widely punctate; bidentate, irregularly toothed, lobed or quadrate between the distal portion of the filament; cup cleft between each stamen for 3-5 mm; teeth when present acute or obtuse,  $\leq 2$  mm long; each stamen (5-) 6-7 (-7.5) mm wide tooth-to-tooth or lobe-to-lobe; distal portion of filament subulate, (4.5-) 5-6.6 (-7) mm long, (1.8-) 2-2.5 (-3) mm wide at point of dilation; anthers oblong, 4.5-5.5 (-6) mm long, grey-brown; pollen grain 47.7-53.4  $\mu\text{m}$  polar diam, 65.5-73.8  $\mu\text{m}$  longest equatorial diam. Style 5.5-6 (-6.5) cm long, exerted ca. 1 cm beyond the anthers; stigma ca. 2-3 mm wide. Ovary globose-ellipsoid, 6-8.5 (-10) mm long, (4.5-) 5.5-7 (-7.5) mm diam, green; ovules (2-) 5-7 (-8). Capsule 1.5-2 cm long, 2-3 cm wide; pedicels 3-4 cm long; seeds (1-) 2-4 per locule, ellipsoid, 8-10 mm long, 5-6 mm diam, with a lustrous, smooth black testa.  $2n = 46$ .

ETYMOLOGY: The epithet of this new species refers to its handsome aspect when in flower.



DISTRIBUTION AND ECOLOGY: Rich, moist soil in the understory of pre- and lower montane rain forest, chiefly in the Napo and Pastaza drainage of Ecuador (Fig. 5); less frequent in Amazonian Peru and Colombia, the lower "ceja de montaña" of north-central Peru, and upper Huallaga valley of Peru (Fig. 6); rare in central Colombia [a single, poorly documented collection (Killip s. n., COL) from near Popayan may be of cultivated origin], 100-1800 m; flowering most commonly January-March. A poultice of the bulbs is used to treat tumors (Lawesson et al. 39632); vernacular name: cebolla de la selva, sugkip.

ADDITIONAL MATERIAL EXAMINED: COLOMBIA. **Amazonas:** confluencia de los Ríos Amazonas y Loretoyacu, 12 Apr 1975, Cabrera 3336 (COL); Trapecio amazónico, Loretoyacu River, ca. 100 m, Sep 1946, Schultes & Black 8342 [in fruit] (US); same locality as preceding, Oct 1946, Schultes & Black 8410 [in fruit] (GH, US). **Caqueta:** Morelia, 150 m, 5 Oct 1941, von Sneidern s. n. (S). **Cauca:** Popayan, 25 Jan 1935, Killip s. n. (COL). ECUADOR. **Morona-Santiago:** Road Limón-Macas, ca. km 20 from Limón, primary rain forest and rastrojos, 700-900 m, 26 Mar 1974, Harling & Andersson 12915 (FLAS, GB). **Napo:** Napo, forest, 6 Oct 1939, Asplund 9122 (S); Tena, marshy forest, 21 Oct 1939, Asplund 9488 (S); Limoncocha, 300 m, 22 Jan 1977, Dodson 6636 (SEL); 45 minute walk by trail from Santa Cecilia up Río Aguarico, ca. 350 m, 28 Mar 1972, Dwyer & MacBryde 9699 [in fruit] (MO); Santa Cecilia, rain forest off runway, 340 m, 30 Mar 1972, Dwyer & Simmons 9743 [in fruit] (MO); Cañon de los Monos, ca. 12 km north of Coca, 250 m, Harling & Andersson 11719, GB specimen (GB); path from Río Bueno to Santa Rosa, Harling et al. 7201 (GB); Río Jivino, Limoncocha, 13-15 Mar 1968, Harling et al. 7673 (FLAS, GB); Armenia Vieja at Río Napo, ca. 12 km sw of Coca, 12 Jan 1973,



Holguer 2655 (FLAS, GB); Cañon de los Monos, road Coca-Lago Agrio, ca. 12 km north of Coca, 24 Jan 1973, Holguer 2960 (GB); Santa Cecilia, Lago Agrio-Baeza, ca. 16 km west of Lago Agrio, 27 Feb 1973, Holguer 3532 (FLAS, GB); Río Aguarico west of Detacamento Zancudo at entrance of Río Zancudo, 320 m, very rich soil, 29 Aug 1979, Holm-Nielsen et al. 20168 [in fruit] (AAU); Añangu, Río Napo, 76° 23' W, 0° 32' S, 260-350 m, 27 June 1983, Lawesson et al. 39632 (AAU); 4.2-7.5 km west of Lago Agrio (5-8.2 km east of Río Conejo) near Lago Agrio-Baeza Road, ca. 340 m, 31 Mar 1972, MacBryde & Dwyer 1387 (MO); ex hort, voucher of SEL Acc. 78-1099, collected vicinity Limoncocha, 240 m, 15 Dec 1982, Meerow 1103 (FLAS). **Pastaza:** Mera, ca. 1100 m, 3 Mar 1956, Asplund 19571 (S); Curaray (Jesús Pitishka), virgin rain forest near the posto militar, ca. 200 m, 18 Mar 1980, Harling & Andersson 17374 (FLAS, GB); between Nalpi and Canelo, 26 Feb 1971, Holguer 1504 (FLAS, GB); trail from Indillama to Canelos, 400 m, occasional, 5 Feb 1935, Mexia 6855 (UC, US); on Napo road north of Puyo, 16 Feb 1953, Prescott 438 (NY). **Tungurahua:** valley of Pastaza River, between Baños and Cashurco, 8 hours east of Baños, 1300-1800 m, Hitchcock 21891 (GH, NY, US); vicinity of Río Margarjitas on Canelos trail, 1225 m, 19 Mar 1939, Penland & Summers 142 (US).

PERU. **Amazonas:** Quebrada Huampami, Lugar tseasim, monte al lado nayumpin, 800 ft, 3 Apr 1973, Ancuash 161 (MO); Quebrada de apigkagentsa, Río Cenepa, 720 ft, Kayap 597 (F, MO); Quebrada Cunup, monte cerca a la chacra, 800-850 ft, 24 Jul 1974, Kayap 1298 [in fruit] (MO); Río Cenepa, vicinity of Huampami, ca. 5 km east of Chávez Valdivia, ca. 78° 30' W, 4° 30' S, Quebrada Aintami, 17 Aug 1978, Kujikat 415 (MO). **Loreto:** Maynas, Yanamono, Explorama Tourist Camp, Río Amazonas, between Indiana and mouth of Río Napo, 72° 48' W, 3° 28' S,

120 m, 18 August 1980, Gentry et al. 29867 (MO); same locality as preceding, 130 m, 18 Feb 1981, Gentry et al. 31418 (MO); Maynas, Iquitos, Río Ampiyacu, 4 vueltas de Monona Cocha, 4 Aug 1976, Revilla 990 (MO); Alto Amazonas, Yurimaguas, Camino a "Shunguyco," al sur-este de Puerto Arturo, cerca a Yurimaguas, 150-200 m, 1 Dec 1984, Schunke 14157 (FLAS). **San Martín:** Mariscal Cáceres, Tocache Nuevo, Camino a Shunté, 12 Mar 1970, Schunke 3856 (F); Lamas, Alonso de Alvarado, San Juan de Pacaizapa, km 72, carretera Tarapoto-Moyobamba, 1000-1050 m, 9 Jun 1977, Schunke 9675 (F); Lamas, Alonso de Alvarado, Fundo Las Malvinas, carretera Moyobamba-Tarapoto, km 43, 850 m, 6 Dec 1984, Schunke 14174 (FLAS); San Roque, in humid loam, 1350-1500 m, 5 Feb 1930, Williams 7748 (F).

Eucharis formosa is the most commonly encountered species in eastern Ecuador (Fig. 5). It extends into Amazonian Peru and Colombia, and also occurs in the lower "ceja de montaña" forests of north-central Peru (Fig. 6). Like the closely related E. candida, E. formosa has a wide elevational range, though this may be in part the result of cultivation. The flowers emit a mild and not particularly pleasant "sour" odor. The biological relationship of E. formosa to E. candida has been discussed under E. candida. Eucharis formosa is larger in all parts than E. candida, and generally has more ovules per locule. The conspicuously horned apiculum is characteristic of Ecuadorean populations of E. formosa (Figs. 2A-B); this character is not obvious in Peruvian collections. Forms with toothed or edentate staminal cups occur throughout this species' range without any observable geographic pattern (Fig. 4B). In cultivation, flowers of the same inflorescence can vary for this character. A Peruvian collection (Schunke 14174)

shows some karyotypic (see Chapter VII) and allozyme divergence (see Chapter VIII) from Ecuadorean populations. In floral morphology (Fig. 7F), however, it is virtually indistinguishable from other Ecuadorean material. A second collection (Schunke 14171) from the same general vicinity of Peru as Schunke 14174 has only shallowly plicate leaves and reduced pigmentation of the staminal cup (Figs. 7D-E). At the present time, I do not believe that enough is known about E. formosa in Peru to justify recognition of subspecific taxa.

3. EUCHARIS BAKERIANA N. E. Brown (Fig. 8). Gard. Chron. 7: 416, Fig. 61. 1890. TYPE: ex hort Sander and Co., Colombia, no other data, 1890, s. n., in part (holotype: K!). Urceolina bakeriana (N. E. Brown) Traub. Pl. Life 27: 57-59. 1971.

Bulb to ca. 5 cm diam, tunics brown. Leaves 2-4; petiole 15-17, 25-30 cm long, 5, 10-11 mm wide; lamina elliptic, 24-29.5, 44-55 cm long, 10, 17-20 cm wide, somewhat succulent, smooth. Scape 6-8 dm tall, ca. 1 cm diam proximally, 5-7 mm diam distally; bracts ovate-lanceolate, 30-38 mm long, ca. 10 mm wide at the base. Flowers 5, 10; with a mild, sweet fragrance, pedicels 10-30 mm long; tube 35-40 mm long, 2-3 mm wide for most of its length, abruptly dilated near the throat to 9-9.7 mm wide, curved abruptly just above the ovary and straight for the rest of its length, thus perpendicular to the vertical axis of the scape; limb spreading to 50-60 mm wide; outer tepals 28.5-32 mm long, ca. (10-) 16.8 mm wide, ovate-lanceolate to ovate, apiculate; inner tepals 26-30 mm long, (14-), 20-22 mm wide, ovate, acute to minutely apiculate. Staminal cup sub-cylindrical to campanulate, ca. 16 mm long (to apex of teeth), 13-15 mm wide, slightly plicate between the filamental trace, very shallowly cleft between each stamen (< 1 mm), proximally marked

green, obtusely bidentate between each free filament; teeth 2-3 mm long, half the length of the subulate portion of the free filament; each stamen 5-6.4 mm wide tooth to tooth; subulate portion of the filament 3-4.5 mm long, 1.5-1.7 mm wide; anthers oblong, 5.4-6 mm long; pollen grain ca. 50.7  $\mu$ m polar diam, ca. 76.9  $\mu$ m longest equatorial diam. Style 45-54.5 mm long, exerted just slightly past the anthers; stigma 2.4-2.8 mm wide. Ovary ellipsoid, 6.5-7 mm long, 5.3-6.5 mm diam; ovules 2-3, 8-9 per locule. Capsule ca. 1.5-2 cm long, 2.5-3 cm wide; seeds ellipsoid, ca. 1 cm long, 0.5 cm diam, with a lustrous, smooth black testa.  $2n = 46$ .

DISTRIBUTION AND ECOLOGY: Very rare in the understory of lower montane rain forest in the middle Río Huallaga valley of Peru, 800 m (Fig. 6). Living material from which the type specimen was prepared was reportedly collected in Colombia. Flowering season not known.

ADDITIONAL MATERIAL EXAMINED: PERU. **San Martin:** 17 km NE of Tarapoto on road to Yurimaguas, trail along stream to waterfall, wet premontane forest on rocky hills, 6° 30' S, 76° 20' W, 800 m, 21 Jul 1982, Gentry et al. 37852 [in fruit] (MO); vicinity of Tarapoto, no other data, flowered in cultivation from material collected by L. Besse, Meerow 1108 (FLAS).

The type of E. bakeriana was prepared from living material supposedly collected in Colombia. When I examined the type specimen, only the several large flowers present in the fragment packet resembled the figure which accompanied Brown's (1890) description of E. bakeriana. The mounted material was referable to the smaller flowered E. candida. At the time, I thought that E. bakeriana might represent an aberrant form of E. candida. Several years later I received bulb of a Eucharis

collected near Tarapoto, Peru by Libby Besse of SEL. When this plant was flowered, the flowers bore exacting resemblance in habit and staminal cup morphology to E. bakeriana, though with considerably more ovules per locule. At present, E. bakeriana is known only from the type, the Besse material, and a fruiting specimen referred to this species on the basis of leaf size.

Eucharis bakeriana is distinct from E. formosa, its closest phenetic and cladistic relative, by its non-pendent flowers which are perpendicular to the vertical axis of the scape, very shallowly cleft staminal cup (< 1 mm, > 2 mm in E. formosa), short subulate portion of the stamen, and sweet floral fragrance (slightly fetid in E. formosa). In leaf size and karyotype, E. bakeriana is very similar to Peruvian material of E. formosa (Schunke 14174, see Chapter VII), but differs by its greater number of subtelocentric chromosomes and the submetacentric morphology of the second-largest pair. The leaves are only shallowly, if at all, plicate, and thicker. As more collections of Eucharis are made, a more realistic idea of the range of E. bakeriana may emerge.

4. EUCHARIS BONPLANDII (Kunth) Traub (Fig. 9). Pl. Life 7: 40. 1951. Hymenocallis bonplandii Kunth. Enum. Pl. 5: 666. 1850. TYPE: Colombia, Río Magdalena, near Nares, Bonpland 1657 (holotype: P!, photo of type: NY!). Caliphruria bonplandii (Kunth) Baillon. Bull. Mens. Soc. Linn. Paris 143: 1136. 1894. Urceolina bonplandii (Kunth) Traub. Pl. Life 27: 57-59. 1971.

Bulb sub-globose, 41-46 mm long, 29-32 mm wide, neck ca. 18 mm long and wide, tunics brown. Leaves 2, somewhat succulent; petiole 8-14 (-18) cm long, 6-8 mm thick proximally, 3-4 mm distally, always shorter than the lamina; lamina elliptic, (16-) 18-24 (-26) cm long, 8.5-11.5 cm



wide, blueish-green, especially in strong light, and slightly glaucous adaxially; lighter green abaxially, the abaxial cuticle densely striate; apex acute to shortly acuminate; attenuate at the base. Scape 4.5-5.8 dm tall, 6-8 mm diam proximally, 3-4 mm diam distally; bracts (25-) 33-40 mm long, ovate-lanceolate, greenish-white. Flowers 5-7, non-fragrant, pendent; pedicels 18-25 mm long; tube 25-33 mm long, 1.8-2.5 mm wide for most of its length, abruptly dilated at the throat to 7-9 (-10) mm wide; limb spreading to 47-55 mm wide; outer tepals ovate-lanceolate, 25.7-30.5 mm long, 8-10 mm wide, apiculate; inner tepals 23-28 mm long, 11.5-14 mm wide, acute to minutely apiculate. Staminal cup sub-cylindrical, (11.5-) 12.5-14.3 mm long (to apex of teeth), 11.5-13 mm wide, stained pale yellow proximally, irregularly bidentate between each free filament, one stamen occasionally only lobed or quadrate, cleft 2.6-4 mm between each stamen; teeth variously acute or obtuse, 1-2 mm long; each stamen 3.6-4.5 mm wide tooth-to-tooth; free portion narrowly subulate, (3.8-) 4.5-5.8 mm long, ca. 1.8 mm wide; anthers 4-4.8 mm long, oblong, greyish-brown; pollen grain ca. 43.5  $\mu$ m polar diam, ca. 63  $\mu$ m longest equatorial diam. Style 50-60 mm long, exerted just beyond the anthers; stigma 2-2.7 mm wide. Ovary sub-globose, ca. 5-6 mm diam; ovules 2-3 per locule.  $2n = 92$ . Capsule ca. 1 cm long, 2 cm wide; seeds 1-2 per locule, ellipsoid, ca. 1 cm long, ca. 0.5 mm diam, with a lustrous black testa.

**DISTRIBUTION AND ECOLOGY:** Rare in central and western Colombia (Fig. 10), in the understory of lower montane rain forest, 400-600 (-1300 m), flowering February-March, May-June, August.

**ADDITIONAL MATERIAL EXAMINED:** COLOMBIA. **Department unknown:** La Mejita [?], June 1844, Goudot s. n. (K, P). **Caldas:** Cauca Valley,



Tabeja, west of Armenia, 1100-1300 m, 23 Jul 1922, Pennell et al. 8604 (GH, NY, US). **Cauca** [?]: La Paila, 30 May 1853, Holton s. n. (NY). **Cundinamarca**: Viotá, Quebrada Cachinibulo, 550 m, 18 Feb 1876, Andre 1583 (K); same locality as preceding, 600 m, 19 Feb 1876, Andre 1721 (K); ex hort, originally collected by J. Paxton near Bogota, ca. 650 m, received from Foster Gardens, Hawaii, 14 May 1982, Meerow 1098 (FLAS). **Tolima**: valle del Alto Magdalena, vereda La Chamba (municipio del Guamo), 400 m, 3 Mar 1963, Uribe 4218 [in fruit] (COL).

Eucharis bonplandii is one of only two tetraploid ( $2n = 92$ ) species in the genus. The species is known only from Colombia, and is rarely encountered. The relative rarity of this species might suggest an autopolyploid origin for E. bonplandii [viz. Stebbins (1951, 1985) hypothesis that autopolyploids rarely are markedly successful in nature], perhaps from an ancestor close to E. ulei, to which, among Amazonian species, E. bonplandii has the greatest phenetic relationship. (see Chapter VI). Meiotic pairing relationships would be helpful in confirming this hypothesis, but unfortunately are difficult to obtain from in these plants. The cladistic hypothesis (Chapter XI) that E. bonplandii and E. bouchei form a monophyletic group (largely on the basis of tetraploidy) is not conclusive.

It may separated from E. ulei by its succulent, glaucous leaves and short petioles. The staminal cup of E. bonplandii is pigmented pale yellow at its base; that of E. ulei is marked green. Eucharis bonplandii and E. lehmanii are the only two species of subg. Eucharis that occur in western Colombia.

5. *EUCCHARIS BOUCHEI* Woodson and Allen (Fig. 11).

Plant 5-6 dm tall. Bulb sub-globose, 30-45 (-85) mm long, (25-) 30-40 (-50) mm diam; neck short, to 25 mm long, 10-20 mm wide; tunics brown. Leaves 1-3 (-4); petiole (9-) 15-25 (-28) cm long, 7-8 mm wide proximally, 5-6 mm wide distally; lamina widely (ovate-) elliptic, (17-) 20-25 (-40) cm long, (7-) 8-10 (-14) cm wide, shortly acuminate, slightly succulent, lustrous bright green adaxially, dull pale green abaxially, smooth, margins mostly non-undulate, abaxial cuticle largely devoid of striation. Scape ca. (4-) 5.5 dm tall, ca. 1 cm diam proximally, ca. 5 mm diam distally; bracts ovate-lanceolate, 25-36 (-47) mm long, (5-) 7-10 mm wide at the base. Flowers (3-) 5 (-6); usually pendent, sometimes only declinate, not fragrant; pedicels 5-10 (-20) mm long, very rarely less than 5 mm; tube (25-) 33-45 mm long, cylindrical and (1.5-) 2-2.5 (-3) mm for most of its length, abruptly dilated near the throat to (7-) 8-10 (-12) mm wide, usually curved gradually, but sometimes only curved abruptly at the base, in which case nearly straight for most of its length; tepals spreading widely from the throat (ca. 90°) or sometimes only at an angle of 45-60°; outer tepals ovate-lanceolate, (18-) 21-28 (-32) mm long, 8-11 (-15) mm wide, apiculate; inner tepals ovate, (16-) 20-26 (-32) mm long, (10-) 12-15 (-17) mm wide, obtuse to acute. Staminal cup sub-cylindrical, 9-12 (-15) mm long to apex of filament, (10-) 12-15 (-18) mm wide, deeply cleft between each stamen to 3-5 mm, usually edentate but variably lobed, acutely or obtusely bidentate, or irregularly toothed between each stamen, marked pale green to greenish-yellow proximally; each stamen (3.5-) 4-5 mm wide at the base, 4-6 (-7) mm long, either trapezoidal in shape (in which case dilating gradually from apex to base), or abruptly dilated at 1/2

to 1/4 of its length (in which case the upper portion narrowly subulate and 2-3 or 3-4 mm long, 1.5-2 mm wide); anthers oblong, 3.5-4.5 mm long; pollen grain 45.7-49.65  $\mu$ m polar diam, 66.8-68.43  $\mu$ m longest equatorial diam. Style (30-) 45-60 mm long, exerted 0.5-1 cm beyond anthers; stigma 2-3 mm wide. Ovary globose or ellipsoid and deeply trigonous, rarely not trigonous, 5-8 mm long, 4-6 (-6.5) mm diam, usually wider than long when deeply trigonous; ovules 2-3 (-4, very rarely 5) per locule, superposed in the lower half of the cell. Capsule 1.5-2 cm long, 2-3 cm wide; pedicels 15-27 mm long; seeds 1-2 per locule, ellipsoid, ca. 1 cm long, 0.5 cm diam, with a lustrous, smooth, black testa.  $2n = 92$ .

Key to the varieties of E. bouchei:

1. Staminal cup edentate, or occasionally with one obscure tooth at the base of one stamen; stamens trapazoidal and gradually dilated from apex to base, or, if obscurely constricted distally, subulate portion > 2 mm wide; Coclé and Colon provinces of Panama, rare in Panama province and in Costa Rica and Guatemala ..... 5a. var. bouchei
1. Staminal cup lobed or toothed; stamens abruptly constricted distally at 1/2-1/4 length into a subulate portion 1.5-2 mm wide.
  2. Outer tepals 26-32 mm long; staminal cup irregularly toothed, the teeth acute; subulate portion of filament 3.5-4.5 mm long; ovary not deeply trigonous; ovules 2-4 per locule; Coclé province of Panama near El Valle ..... 5b. var. dresslerii

2. Outer tepals 20-26 mm long; staminal cup obtusely bidentate or lobed; subulate portion of filament  $\leq 3.5$  mm long; ovary deeply trigonous; ovules 2-5 per locule; Panama and Darien provinces of Panama, rare in Guatemala .....  
 ..... 5c. var. darienensis

5a. Eucharis bouchei var. bouchei Woodson and Allen (Figs. 11Aii-iii, B-C). Ann. Missouri Bot. Gard. 24: 181. 1937. TYPE: Panama, Coclé, El Valle de Antón, 500-700 m, 23-27 Jul 1935, Seibert 466 (holotype: MO!). Urceolina bouchei (Woodson & Allen) Traub. Pl. Life 27: 57-59. 1971.

Perianth tube (30.8-) 34-45 mm long; outer tepals (18-) 24-28 (-35) mm long, (8.8-) 9.4-15.5 mm wide; inner tepals 21-26 (-31) mm long, 11-17.5 mm wide. Staminal cup (8, 9-) 11.5-15 (16.7) mm long (to apex of filaments), (9-) 12-15.5 (-16, 18) mm wide, edentate or rarely with a single obscure tooth between one or several stamens; each stamen trapezoidal in shape, dilating gradually from the apex to the base, or, if obscurely constricted in the distal 2-3 mm, the subulate portion wider than 2 mm. Style exerted ca. 1 cm beyond the anthers. Ovary trigonous; ovules 2-3 per locule.

DISTRIBUTION AND ECOLOGY: Understory of primary, pre- and lower montane rain forest in Coclé and Colon provinces of Panama (Fig. 12), particularly in the vicinity of El Valle de Antón and the Río Guanche valley; rare in Panama province, Costa Rica and Guatemala (Fig. 13); frequently on steep slopes; (200-) 500-1000 m; flowering (March) June-August, October-December.

ADDITIONAL MATERIAL EXAMINED: COSTA RICA. **Puntarenas:** Canton de Osa, hills near Palmar Norte, Río Grande de Terraba, 2000 ft, Allen 5347

(F, K, MO, US); cataratas de San Ramón, 26 Feb 1931, Brenes 13515 (F).  
**San Jose:** El Rodeo, Mar 1931, Lankester s. n. (F). GUATEMALA.  
**Suchitepequez:** Finca Mocá, steep, bushy slope, 3300 ft, 31 Oct 1934, Skutch 1585 (F). PANAMA. Coclé: lower Río Antón, vic. El Valle de Antón, 800-1000 m, 30 Dec 1936, Allen 120 (GH, MO); vic. of El Valle de Antón, 600-1000 m, Allen 1228 (GH, MO); vic. El Valle de Antón, ca. 600 m, 10 Dec 1939, Allen 2063 (MO); hills north of El Valle de Antón, 100 m, 14 Aug 1940, Allen 2182 (MO); region north of El Valle de Antón, ca. 1000 m, 21 Aug 1946, Allen 3641 (G); La Mesa, above El Valle, 600-800 m, 18 Jan 1968, Duke & Dwyer 15180 [in fruit] (NY); 1-3 miles west of Portobello, Gentry 1750 (MO); foot of Cerro Pilon, 11 Jan 1972, Gentry & Dwyer 3634 [in fruit] (F, MO); foot of Cerro Pilon, 11 Jan 1972, Gentry & Dwyer 3636 [in fruit] (MO); El Valle de Antón, along Río Indio Trail, 500-700 m, Hunter & Allen 338 [in fruit] (G, MO, P, US); El Valle de Antón, 1000-2000 ft, edge of cloud forest and roadside, Dec 1967, Lewis et al. 2617 (MO); ex hort, from bulb collected by M. Whitten and M. Elliot, vic. El Valle, flowered in cultivation, 25 Jul 1984, Meerow 1125 (FLAS); Cerro Pilon, 5 km north of El Valle, 800-1045 m, 13 Jun 1975, Mori et al. 6586 (AAU); Quebrada Amarillo, north of El Valle, 17 Oct 1975, Witherspoon & Witherspoon 8736 (MO). **Colon:** Río Guanche, 16 Nov 1975, D'Arcy 9679 (MO); hills just north of Río Guanche, 1-200 m, 16 Nov 1975, Davidse & D'Arcy 10096 [in fruit] (MO); Cerro Brujo, ex hort, collected by R. Dressler, flowered in cultivation, Jul 1985 Meerow 1157 (FLAS); trail south of Río Guanche, on ridge to Cerro Pan de Azucar, 200 m, Mori & Kallunki 2014 (AAU); Río Guanche, 6 Nov 1974, Mori & Kallunki 3019 [in fruit] (AAU). **Panama:** mountains above Torti Arriba, 2 Dec 1977, Folsom et al. 6582 (AAU, BM, MO); near Cerro Campana, on trails



radiating from end of road which passes Campana water tank, 23 Aug 1967, Kirkbride & Hayden 305 (MO, NY).

5a. Eucharis bouchei var. dresslerii Meerow, var. nov (Fig. 11Ai).

Varietas haec ab varietas typica differt staminibus acute dentatis ad 1.5-2 mm distale constrictis, ovario non trigono, et ovulis in quoque loculo aliquando plurimioribus. TYPE: ex hort, from bulbs collected by R. Dressler in Panama, Coclé, El Valle de Antón, flowered in cultivation, 17 Mar 1983 Meerow 1107 (holotype: FLAS!).

Perianth tube 30-41 mm long; outer tepals 26.2-32 mm long, 6-10 mm wide; inner tepals 24-28 mm long, 9-13.5 mm wide. Staminal cup 10-16 mm long (to apex of filaments), 9.5-11.5 mm wide, irregularly toothed (some stamens lobed or quadrate), the teeth acute and from 1.5-2.7 mm long; each stamen distally constricted abruptly at 1/2 length, the subulate portion 3.5-4.5 mm long, ca. 1.8 mm wide. Style exerted ca. 0.5 cm beyond the anthers. Ovary not trigonous; ovules 2-4 per locule.

ETYMOLOGY: This variety is named in honor of Robert L. Dressler, well-known tropical biologist.

DISTRIBUTION AND ECOLOGY: Rare rain forest understory herb in Coclé province of Panama (Fig. 12), in the vicinity of El Valle de Antón, perhaps sympatric with var. bouchei, ca. 900 m; flowering in June.

ADDITIONAL MATERIAL EXAMINED: El Valle de Anton, 900 m, 4 Jun 1939, Alston 8727 (BM).

5c. Eucharis bouchei var. darienensis Meerow, var. nov.

Varietas a Eucharis bouchei var. dresslerii affinis sed differt staminibus obtuse dentatis vel lobis et parte staminea distale subulata brevior. TYPE: Panama, Darien, valley between Cerro Pirre and next most southerly peak, Jul 1977, Folsom 4402 (holotype: MO!).



Perianth tube 25.5-36 (-43.4) mm long; outer tepals 20-26 mm long, 8-11 mm wide; inner tepals 10.5-24 mm long, (11-) 12-15 (-16.5) mm wide. Staminal cup 9-10 (-13, 16) mm long (to apex of filaments), 12-14.5 (18) mm wide, obtusely bidentate or lobed, the teeth when present ca. 1-1.5 mm long; each stamen distally constricted abruptly at 1/2-1/4 length; the subulate portion ca. 1.7-3 mm long, 1.5-2 mm wide. Style exerted less than 0.5 cm beyond the anthers. Ovary trigonous; ovules 2-5 per locule.

ETYMOLOGY: The varietal epithet refers to Darién province of Panama, where E. bouchei var. dariensis is most frequently collected.

DISTRIBUTION AND ECOLOGY: Understory of primary rainforest in Darien province of Panama (Fig. 12); rare in Panama province and Guatemala (Fig. 13); 480-1450 m; flowering January-February and June-August (-November).

ADDITIONAL MATERIAL EXAMINED: GUATEMALA. **Solola:** between St. Pedro and Sta. Lucia, 20 Jan 1857, Wendland 207 (GOET). PANAMA. **Darien:** La Boca de Pirre, 13 Oct 1967, Bristan 1285 [in fruit] (MO); vicinity of airstrip at Cana gold mine, 480 m, disturbed forest, 29 July 1976, Croat 37956 (AAU); Cerro Pirre, cloud forest and/or mossy forest, 2500-4500 ft, Aug 1967, Duke & Elias 3661 (GH, MO, US); Cerro Tacarcuna, south slope, 1250-1450 m, 26 Jan 1975, Gentry & Mori 13945 (MO); 0-2 miles east of Tres Bocas, along shortest headwaters of Río Cuasi, premontane rain forest, 28 Mar 1968, Kirkbride & Duke 1175 [in fruit] (MO); vicinity Cana, 1750 ft, rare on forest floor, 23 June 1959, Stern et al. 499 (GH); gold mine at Cana, 480 m, 26 Jul 1976, Sullivan 626 [in fruit] (MO); trail northwest of Cana, 600 m, 28 Jul 1976, Sullivan 718 [in fruit] (MO); gold mine at Cana, 480 m, 29 Jul 1976, Sullivan 753 [in

fruit] (MO); Cana-Cuasi trail, Chepigano, 2000 ft, 12 Mar 1940, Terry & Terry 1533 [in fruit] (F). **Panama:** stream flowing out of Serrania de Maje, 10 Feb 1977, Folsom & Collins 1725 [in fruit] (MO); Maje, 5 miles up Río Maje, steep forested ridge above Chocó Indian trail, 400 m, 19 Nov 1970, Kennedy 680 (MO, US); woods around La Eneida, 1000 m, 5 Aug 1970, Luteyn & Kennedy 1761 [in fruit] (F); lower slopes and trail to Cerro Campana, 13 Sep 1975, Witherspoon & Witherspoon 8372 (MO).

Eucharis bouchei is the northernmost distributed species of Eucharis, and the only species found north of the Darien Gap. It is also the most variable species in the genus, in characteristics that elsewhere justify specific delimitation. Patterns of variation in floral size, and tube and limb habit form a complete mosaic throughout the range of E. bouchei, and show little or no geographic consistency. Staminal cup morphology (Fig. 4C) does, however, demonstrate a fair degree of geographical consistency, and it is chiefly on this basis that I have recognized var. bouchei and var. darienensis. Variety dresslerii, rarely encountered among populations of var. bouchei, presents a special case, discussed below.

The unprecedented degree of variation in E. bouchei is likely the result of two main factors: (1) the species is tetraploid, putatively allotetraploid (see Chapters VII and VIII for detailed discussion), and (2) probably represents a geologically recent colonization of Central America by this primarily northern Andean and Amazonian genus (see Chapter IX for detailed discussion). Eucharis bouchei is thus a highly heterozygous, allotetraploid, semi-species complex still in the process of active evolution. The wide variation present in E. bouchei likely represents the segregating phenotypes of a richly diverse genetic base.

On the basis of known distributions (Figs. 12-13), it appears that substantial geographic barriers exist between groups of populations, probably restricting gene flow between them. Left undisturbed, as is not the case in the Neotropics today, these aggregates could conceivably each justify specific recognition.

Northwesternmost populations representing var. bouchei have the most derived androecial morphology (Figs. 4Ci-ii) relative to southeasterly populations (var. darienensis, Fig. 4Civ). The latter have staminal cups similar to the generalized morphology characteristic of Andean and Amazonian species of subg. Eucharis. This suggests to me that general movement of E. bouchei in Central America has been away from the Colombian border. The occasional presence of E. bouchei in Costa Rica is not surprising, but the two reported collections from Guatemala (Wendland 207 and Skutch 1585) represent a substantial disjunct. This is all the more interesting due to the fact that each of the two represents a different variety of the species. Given the history of cultivation of Amazonian Eucharis by Indian people for medicinal, ceremonial and possibly ornamental use, the same may have held true in Central America.

Variety bouchei, most common around El Valle de Antón in Coclé province, is recognized by its largely edentate staminal cup in which the trapezoidal free filament is not markedly constricted distally into a narrow subulate portion (Figs. 4Ci-ii, 11C). The staminal cup of variety darienensis, found both in Panama and Darien provinces, is obtusely bidentate or lobed (Fig. 4Civ). The free filament constricts distally into a narrow (< 2 mm) subulate portion. These two varieties

occur in close proximity in one location, near Cerro Campana in Panama province (Fig. 12).

The rare var. dresslerii (Fig. 11Ai), with its acutely toothed staminal cup (Fig. 4Ciii) and non-trigonous ovary, may be the result of recent sympatric divergence, as it occurs in close geographic proximity to populations of var. bouchei. This variety is an unstable tetraploid, producing at least some cells with diploid ( $2n = 46$ ) chromosome number (see Chapter VII). This variety also does not express an additive banding phenotype for an aspartate amino transferase (AAT-2) locus, which otherwise characterizes electrophoretic phenotypes of E. bouchei. Electrophoretic phenotypes also suggest profound genetic divergence from var. bouchei. Genetic identity (Nei, 1978) between the two varieties is only 0.632-0.807, considerably below that which is usually characteristic of conspecific plant populations (Gottlieb, 1977).

Eucharis bouchei offers an excellent opportunity for detailed study of the evolution of a tropical rain forest organism. Future work should seek to quantify in greater detail the genetic variation present within and among populations of this actively evolving species complex. I have so far been unsuccessful in obtaining meiotic pairing figures from limited dissection of bulbs, information that would be helpful in confirming the nature of this species' polyploid origins.

6. EUCHARIS ASTROPHIALA (Ravenna) Ravenna (Fig. 14). Phytologia 57: 95-96. 1985. Urecolina astrophiala Ravenna. Pl. Life 38: 49. 1982. TYPE: Ecuador, Cotopaxi, Quevedo-Latacunga road, km 46 from Quevedo, 79°11'W, 0°55'S, 600 m, 4 Apr 1973, Holm-Nielsen et al. 2851. (HOLOTYPE: AAU; ISOTYPE: S!)

Bulb globose, 4-5 cm long, 3-4 cm wide, usually without an appreciable neck, tunics tannish-brown. Leaves 2-4 at anthesis, elliptic- or ovate-lanceolate; petiole 10-20 cm long, 4-5.5 mm thick; lamina 15-25 cm long, 5-10 cm wide, thin, non-lustrous, deeply plicate and pustulate, adaxial surface light green, the white midrib conspicuous; abaxial surface whitish-green; margin slightly undulate; apically acuminate; basally attenuate to the petiole. Scape 3-4 (-5) dm tall, ca. 5 mm diam; bracts 29-35 (-40) mm long, lanceolate. Flowers 5-8 (-10); pedicels 8-14 mm long; tube 28-35 mm long, ca. 2 mm wide for most of its length, dilating to (4-) 5-6 mm at the throat, strongly curved; perianth limb spreading to 4-5 cm wide; outer tepals 25-30 mm long, (7-) 10 mm wide, lanceolate, apiculate; inner tepals 25-28 mm long, 10-12 (-14) mm wide, ovate-lanceolate to ovate, acute. Staminal cup funnelform-cylindrical, (10-) 12-14 mm long, 8-12 mm wide, edentate, stained orange-yellow basally, cleft between each stamen for 1/2-2/3 of its length; each free filament (5) 6.4-6.9 mm long, ca. (2.5-) 3.5-4.5 mm wide at the base, deltoid; anthers oblong, 5-5.5 mm long; average pollen grain 58.6-60.6  $\mu$ m polar diam, 83.0-86.1  $\mu$ m longest equatorial diam. Style 50-55 mm long, exerted 5-10 mm beyond the staminal cup; stigma 3-lobed, ca. 2 mm wide. Ovary globose-trigonous, 3.9-4.5 mm long, 3.2-4 mm wide, white at anthesis; ovules 2-3(-4) per locule, medially superposed. Capsule ca. 1-1.5 cm long, 2-2.5 cm wide; seeds 1-2 per locule, ellipsoid, ca. 1 cm long, 0.5 cm diam, with a lustrous, smooth black testa.  $2n = 46$ .

**DISTRIBUTION AND ECOLOGY:** Endemic to the western declivity of the Andes in north-central Ecuador (Fig. 15), particularly in contiguous areas of Cotopaxi, Los Rios and Pichincha provinces, occupying the



understory of lower montane rain forest from (250-)400-800(-1100) m elevation. Sporadic flowering may occur at any time but is concentrated in the wetter months of the year. Unlike the species of subgenus Eucharis from Amazonas, E. astrophiala manifests a definite rest period when growth ceases, though the leaves may persist for the duration.

ADDITIONAL SPECIMENS EXAMINED: ECUADOR. **Bolivar:** Limon, 800-1100 m, 14 Oct 1943, Acosta-Solis 6374 (F). **Chimborazo:** km 52-53 on Quevedo-Latacunga road, Tenefuerste, Río Pilalo, Tenefuerste, 750 m, 21 Feb 1982, Dodson & Gentry 12815 (MO, SEL); same locality as Dodson & Gentry 10187, 23 May 1983, Dodson & Gentry 13793 (MO, SEL); Puente de Chimbo, 250 m, Jun 1876, Lehmann 7775 (K). **Cotopaxi:** km 40 on road from Quevedo to Latacunga, 600 m, 6 Mar 1975, Dodson 5864 (MO, SEL, US); 3 km east of El Palmar on Quevedo-Latacunga rd, 800 m, 5 Apr 1980, Dodson & Gentry 10187 (MO, SEL); same locality as Dodson & Gentry 12815, 750 m, sterile, 15 Aug 1984, Meerow & Meerow 1140 (FLAS). **Los Rios:** forested hills 12 km east of Patricia Pilar, 650 m, 9 Apr 1977, Madison 3792 (NY). **Pichincha:** Centinela, Canton Santo Domingo, km 12 east of Patricia Pilar, 600 m, 17 Aug 1978, Dodson et al. 7122 (MO, SEL); 2 km SE of Santo Domingo de los Colorados along Río Verde, 530 m, 5 Feb 1979, Dodson & Duke 7714 (MO, SEL); road from Patricia Pilar to 24 de Mayo at km 12, path following ridge line at El Centinela at crest of Montañas de Ila, 600 m, 6 Apr 1980, Dodson & Gentry 10298 (MO, SEL); Reserva Endesa, ca. 6 km WNW of P. Vicente Maldonado, mature rain forest, ca. 800 m, 24 Mar 1985, Harling & Andersson 23279 (GB); Santo Domingo de los Colorados, Rancho Brahman, ca. 10 km NW of the town on road to Esmeraldas, 400 m, 31 Mar 1967, Sparre 15216 (S).



Eucharis astrophiala is easily separated from the other small-flowered species of subg. Eucharis by its uniquely bullate-pustulate and non-lustrous ovate-lanceolate leaves; edentate and deeply cleft staminal cup with deltoid free filaments (Fig. 14B-C); and large pollen grain (the largest in the genus) with narrow reticulum muri. The largest chromosome pair of E. astrophiala is submetacentric, unlike all other species of the genus I have examined. It is the only species of the subgenus found exclusively on the western slopes of the Andes south of Colombia. It occurs sympatrically in some localities (fide Dodson & Gentry 12815 and Meerow & Meerow 1140) with E. anomala, though the latter grows at slightly higher elevation in these areas. Eucharis astrophiala is the only species of subg. Eucharis that enters a definite rest period during the short dry season of the north- and central western Ecuadorean Andes. New growth completely ceases, though 1-2 leaves may persist for the duration.

7. ECHARIS ULEI Kränzlin (Fig. 16B). Bot. Jahrb. 50: Beibl. 111: 4-5. 1913. TYPE: Brazil, Amazonas, Jurua Miry, Jun 1901, Ule 5737a (holotype: B!), non Ule 5737b [in fruit] (B!) vel Ule 5737 (GOEL!). Urceolina ulei (Kränzlin.) Traub. Pl. Life 27: 57-59. 1971.

Eucharis ipariensis (Ravenna) Ravenna. Phytologia 57: 95. 1984. Urceolina ipariensis Ravenna. Pl. Life 38: 50-51. 1982. TYPE: Peru, Huánuco, Pachitea, Honoria, Bosque Nacional de Iparia, Río Pachitea, 20 km above confluence with Río Ucayali, near Miel de Abeja, 1 km from Tuernavista, 26 Apr 1967, Schunke 1887 (holotype: NY; isotypes: F!, COL!, G!, US!).

Eucharis moana (Ravenna) Ravenna. Phytologia 57: 95. 1984. Urceolina moana Ravenna. Pl. Life 38: 50. 1982. TYPE: Brazil, Acre,

Rio Moa at Serra da Moa village, 27 Apr 1971, Prance et al. 12491  
(holotype: NY!, isotypes: K!, MO!, herb. Ravenna).

Plant to 5-6 dm tall. Bulb sub-globose, (2.5-) 3.5-4.5 (-5) cm long, 2-3.5 (-4.5) cm diam; neck 1-2 cm long, ca. 1.5 cm wide; outermost tunics grey-brown, inner tunics tan. Leaves 2-3; petiole (10-) 18-30 (-35) cm long, 5-6 mm thick; lamina (narrowly) elliptic (average length : width > 3), 18-25-33 cm long, (5-) 7-10 (-12.5) cm wide, acute to shortly acuminate, attenuate at the base. Scape (35-) 40-58 cm tall, 8-10 mm diam proximally, 3-4 mm diam distally; bracts lanceolate to ovate-lanceolate, (25-) 30-37 (-54) mm long, greenish-white. Flowers (3-) 5 (-7), pendent, without fragrance; pedicels (8-) 11-15 (-20) mm long, ca. 2 mm diam; tube (25-) 28-35 (-37.5) mm long, curved gradually for most of its length, 1.5-2 (-2.5) mm wide for most of its length, abruptly dilated just below throat to (6-) 7-10 mm; limb spreading to 40-45 (-55) mm wide; outer tepals ovate-lanceolate, 24-28 (-32) mm long, (6.5-) 8-10 (-11) mm wide, apiculate; inner tepals ovate, 23-27 (-30) mm long, (9-) 10-13 (-15) mm wide, acute. Staminal cup funnelform-cylindrical, 10-12 mm long (to apex of teeth or lobes), 11-13 (-16) mm wide, usually bidentate between each free filament, rarely edentate, irregularly toothed, or the teeth obscure (in which case the stamens quadrately lobed), cleft between each stamen for (1.5-) 2-3 (-4) mm, with a + rectangular, green zone in the proximal half of each stamen; teeth acute or obtuse, 0.5-0.7 mm long; each stamen 3.5-4.5 (-5.5) mm wide from tooth to tooth; free filament subulate, (3-) 4.5-6 mm long, (1-) 1.5-2 mm wide at its base; anthers oblong, 3-3.8 mm long; pollen grain ca. 49.35  $\mu$ m polar diam, ca. 69.85  $\mu$ m longest equatorial diam. Style (40-) 45-50 (-60) mm long; stigma 1.5-2.5 mm wide. Ovary globose-ellipsoid,

6-8.5 (-10) mm long, 4-5.5 mm wide; ovules 2 (-4) per locule, superposed in the lower half of the cell. Capsule 1.2-1.5 cm long, 2-2.5 cm wide; pedicels 2-4 cm long; seeds 1-2 per locule, ellipsoid, 8-10 mm long, ca. 5 mm wide with a smooth, lustrous black testa.

**DISTRIBUTION AND ECOLOGY:** Understory of primary rain forest in the Amazon Basin and eastern Andean foothills, most common in Peru but sporadically encountered north to Colombia and south to Bolivia (Fig. 10), on fertile, usually non-inundated, soils; 100-300 (-1000) m; flowering at any time of the year, but most frequently from June-September.

**ADDITIONAL MATERIAL EXAMINED:** BOLIVIA. **El Beni:** Covendo, 600 m, 19 Aug 1921, White 930 (K, NY). BRAZIL. **Amazonas:** basin of R $\acute{o}$  Jurua, Foz da Tarauca, Yuma, rare, on vareza land, 1 Jun 1933, Krukoff 4613 (NY); basin of R $\acute{o}$  Jurua, near mouth of R $\acute{o}$  Embira, 7 $^{\circ}$  30' S, 70 $^{\circ}$  15' W, 3 Jun 1933, Krukoff 4637 [in fruit] (G, GH, K, NY, S, US); R $\acute{o}$  Purus, R $\acute{o}$  Itaxi, Seringal Jurucua, 120 km south of Lábrea, 29 Jun 1971, Prance et al. 13915 (MO, NY). **Para** [?]: no data, Ferreira s. n. (P). COLOMBIA: **Amazonas:** Trapecio, confluencia de R $\acute{o}$  Loretoyacu con el R $\acute{o}$  Amazonas, Puerto Nariño, Mar 1968, Diaz-M 15 (COL); Trapecio amazonico, Boiauassú River, 100 m, Oct 1946, Schultes & Black 8608a (US); Puerto Nariño, mouth of R $\acute{o}$  Loretoyacu, 100m, 8 May 1972, Plowman 3216 [in fruit] (COL, K). PERU. **Amazonas:** valle de R $\acute{o}$  Santiago, ca. 65 km norte de Pinglo, Quebrada Caterpiza, 2-3 km atrás sde la comunidad de Caterpiza, 200 m, 13 Oct 1979, Huashikat 930 [in fruit] (MO); same locality as preceding, 17 Dec 1979, Huashikat 1553 (MO); Monte del Isla, la isla 1 km bajo de La Poza, R $\acute{o}$  Santiago, 180 m, 8 Aug 1979, Leveau 7 [in fruit] (MO); same locality as preceding, 15 Aug 1979, Leveau 123 [in

fruit]; (MO); same locality as preceding, 8 Aug 1979, Peña 9 [in fruit] (MO). **Loreto:** Río Amazonas, SE of Iquitos, swampy forest, 17 Aug 1972, Croat 19289 (MO); Río Napo near Entrada de Isla Inayuga, edge of forest, 20 Sep 1972, Croat 20521 [in fruit] (MO); near Base Araguana, upper Río Mazán, ca. due north of Santa Maria de Nánay, non-inundated forest, 9 Jul 1976, Gentry & Revilla 16586 [in fruit] (MO); Maynas, Quebrada Yanomono, Explorama tourist camp, halfway between Indiana and mouth of Río Napo, mature non-inundated forest on laterite, 4 Nov 1979, Gentry et al. 27438 [in fruit] (MO); Yanomono, Explorama Tourist Camp, Río Amazonas above mouth of Río Napo, 72° 48' W, 3° 28' S, 130 m, upland forest on lateritic soil, 25 Jun 1982, Gentry et al. 37204 [in fruit] (MO); Río Samiria, Flor de Yarina, ca. 5° 2' S, 74° 30' W, 160 m, non-inundated restinga forest, Gentry et al. 38103 (MO); Iquitos, ca. 100 m, 3-11 Aug 1929, Killips & Smith 27442 (US); Yurimaguas, lower Río Huallaga, ca. 135 m, 23 Aug-7 Sep 1929, Killip & Smith 27656 (US); Río Marañón Valley, San Lorenzo, between mouths of Río Pastaza and Río Huallaga, 150 m, 20 Aug-9 Sep 1929, Killip et al. 29227 (US); Iquitos, Muenca-Caño, 105 m, 9 Feb 1932, Mexia 6504a (F, UC); Maynas, Río Amazonas near Tamishiyacu, 3 Sep 1976, Revilla 1281 (MO); Pebas on Amazon River, 25 Jul 1929, Williams 1751 [in fruit] (F); Pebas on Amazon, 21 Jul 1929, Williams 1787 [in fruit] (F); La Victoria on the Amazon, 21 Aug 1929, Williams 2629 (F); same locality as preceding, 29 Aug 1929, Williams 2938 (F); alto Río Itaya (San Antonio), 145 m, Williams 3398 [in fruit] (F); Puerto Arturo, Yurimaguas, lower Río Huallaga, 155-210 m, 16 Nov 1929, Williams 5148 [in fruit] (F). **San Martín:** Mariscal Caceres, Tocache Nuevo, Quebrada de Cachiyacu de Huaguisha, 570 m, 16 Jul 1982, Meerow et al. 1023 [in fruit] (FLAS); Mariscal Caceres, Tocache Nuevo,

Quebrada de Cachiyacu de Huaguisha, 570 m, 16 Jul 1982, Meerow et al. 1024 (FLAS); Mariscal Caceres, Mirama, north of Tocache Nuevo, along left bank of Río Huallaga, 500 m, Plowman & Kennedy 5811 (GH); Mariscal Caceres, Tocache Nuevo, Fundo La Campiña, 2 km abajo de Tocache Nuevo, margen derecha del Río Huallaga, 400 m, 7 Sep 1969, Schunke 3396 (F, US); Mariscal Caceres, Tocache Nuevo, Quebrada de Cachiyacu, 3 km abajo de Puerto Pizano (margen derecha del Río Huallaga), 21 Apr 1971.

**Ucayali:** Coronel Portillo, Yarina Cocha, Fundo "El Pescador," cerca al Caserio Nuevo Destino, al este de Yarina Cocha, 150 m, 31 Oct 1984, Schunke 14153 (FLAS).

Eucharis ulei is among the more widespread Amazonian taxa of subg. Eucharis, extending north from its Peruvian center of distribution into Colombia, and south to Bolivia (Fig. 10). The species is best recognized by its primarily narrow-elliptic leaves, chiefly 5-flowered inflorescence, tube length ca. 3-4 cm, limb spread of 4-5 cm, and reduced ovule number (generally 2 per locule, Fig. 16C). Both flower and ovule number have become nearly fixed throughout the range of the species. In many respects, E. ulei occupies a morphologically intermediate position between the more floriferous E. candida, more common to the north, and the smaller and many-flowered E. castelnaeana and its allies. Eucharis castelnaeana is sympatric with E. ulei at times, but tends to occur on seasonally inundated soils. The fruit of E. castelnaeana is not orange, however, and the seed coat is rugose. Eucharis candida and E. ulei are not at all fragrant, whereas E. castelnaeana produces a faint, sweet fragrance. This, along with size differences, may reflect pollinator-adapted divergence among the three taxa. Flower size and number, ovule number (Fig. 16), and chromosome



morphology (see Chapter VII) suggests close to E. cyaneosperma, which has different tube morphology and blue-coated seeds.

Ravenna (1982, p. 50) described Urceolina moana, citing the "absence of lobes, or teeth, in the cup". When I examined the single, poorly preserved, fragmentary flower of the holotype, however, the stamens appeared at least shortly dentate to quadrate. As in E. candida and E. formosa, androecial toothiness in E. ulei has little taxonomic significance. The androecial morphology of E. moana is well-included within the range of variation for this character in E. ulei (Fig. 4D). Several collections of E. ulei have completely edentate staminal cups (e.g., Meerow et al. 1024, Plowman & Kennedy 5811, Prance et al. 13915). Eucharis ipariensis, inexplicably described by Ravenna (1981) as allied to E. mastersii (= E. X grandiflora of subg. Heterocharis), is indistinguishable from numerous collections of E. ulei.

Both Kränzlin (1913) and Macbride (1939) noted the dissimilarity of the two specimens comprising the holotype of E. ulei (Ule 5737, B), one in flower, the other a fruiting specimen. I have assigned the fruiting specimen (Ule 5737b), with blue seeds, to E. cyaneosperma Meerow. When a putative isotype of Ule 5737 was received from GOEL, it proved to represent E. castelnaeana. Ule thus collected three species under a single number, a not uncommon occurrence in areas where several Eucharis species are sympatric.

8. Eucharis cyaneosperma Meerow, sp. nov. (Fig. 16A).

Species a E. ulei Kränzlin affinis sed differt foliis ellipticis brevioribus, tubo minus arcuato, et testa seminali cobaltina. TYPE: Peru, San Martín, 20 km north of Tocache Nuevo on road to Tarapoto, Río Cañuto, 520 m, 17 Jul 1982, Meerow et al. 1032 (holotype: FLAS!)



Bulb subglobose, 3-5 cm long, 3-3.5 cm diam, tunics light brown. Leaves 2-4; petiole (10-) 15-30 (-35) cm long, 5-6.5 mm thick; lamina (ovate-)elliptic, 18-25 (-30) cm long, (6.5-) 7-8 (-13) cm wide, apically acute to shortly acuminate, attenuate at the base. Scape (3-) 4-5 (-6.5) dm tall, 5-7 mm diam proximally, 3-4 mm diam distally; bracts ovate-lanceolate, (20-) 27-35 mm long. Flowers (3-) 5 (-7), pendent, without fragrance; pedicels (10-) 15-25 (-28) mm long, ca. 1.7-2 mm diam; tube 30-40 mm long, 1.5-2 mm diam for most of its length, dilating abruptly to 7-9 mm proximal to the throat, curved abruptly ca. 5 mm above the ovary and then more or less straight; outer tepals 23-28 (-32) mm long, 8-10 (-13) mm wide, ovate-lanceolate, apiculate; inner tepals 21-24 (-30) mm long, 10-14 (-15) mm wide, ovate, acute to minutely apiculate. Staminal cup cylindrical, (8-) 10-12 mm long (to tooth or lobe), 10-13 (-15) mm wide, pale yellow or green proximally, quadrate or irregularly toothed between each free filament, the teeth when present < 1.5 mm long, cleft between each stamen 2-3 mm deep; each stamen 3.5-4 (-5) mm wide at the base; the narrow, subulate free filament (3-) 3.5-4.5 (-5.5) mm long, ca. 1.5 mm wide at the base; anthers ca. 3 mm long, oblong; pollen grain ca. 47.95  $\mu$ m polar diam, ca. 67.55  $\mu$ m longest equatorial diam. Style 4.5-6 cm long, exserted 0.5-1 cm beyond the anthers; stigma 2-2.5 mm wide. Ovary sub-globose-trigonous, 5-7 mm long, 7-10 mm wide, usually wider than long; ovules 2 (-3, 5) per locule, superposed in the lower half of the cell. Capsule 10-12 mm long, 15-20 mm wide; pedicel 25-36 mm long; seed ellipsoid, 7-9 mm long, ca. 5 mm wide, with a lustrous, cobalt-blue testa.  $2n = 46$ .

ETMOLOGY: The specific epithet refers to the cobalt-blue seed coat of this species.

DISTRIBUTION AND ECOLOGY: Rare in the understory of pre- to lower montane rain forest of the Amazon basin and eastern Andean foothills, from Peru to Bolivia (Fig. 10), (330-) 400-800 (-1200) m elevation, flowering at any time of the year but most commonly in August.

ADDITIONAL MATERIAL EXAMINED: BOLIVIA. **El Beni:** vicinity of Rurrenabague, 330 m, 25 Nov 1921, Cardenas 1179 (AA, NY, US); Rurrenabague, 500 m, 7 Oct 1921, Cardenas 1553A (NY); San Antonio, 15 Nov 1958, flowered in cultivation 30 Apr 1959, Nelson 58-301 (MO); same collection as preceding, flowered in cultivation 4 Apr 1961, Nelson 58-301 (MO). BRAZIL. **Acre:** basin of Rio Purus, near mouth of Rio Macauhan, 9° 20' S, 69° W, 17 Aug 1933, Krukoff 5573 (NY); Rio Branco de Obidos, Santo Antonio, 6 Aug 1912, Ducke 12162 (GOEL, photo and fragment F). **Amazonas:** Jurua Miry, Jun 1901, Ule 5737b (B). PERU. **Cuzco:** Rio Araya, northeast of Cuzco, 1150 m, Jan 1943, Sandeman 3724 (K, OXF). **Loreto:** lower Rio Nanay, 24 May 1929, Williams 431 [in fruit] (F); La Victoria on Amazon, 21 Aug 1929, Williams 2619 [in fruit] (F); La Victoria on Amazon, 28 Aug 1929, Williams 2878 [in fruit] (F, US). **Junin:** Puerto Yessup, ca. 400 m, 10-12 Jul 1929, Killip & Smith 26394 [in fruit] (F, NY, US); Rio Negro to Satip, 800 m, 17 Aug 1960, Woytkowski 5830 (MO). **Madre de Dios:** Tahuamanu, Iberia, 200 m, 15 Nov 1973, Alfaro 1684 [in fruit] (MO); Iberia, Miraflores, vicinity Rio Tahuamanu, 1 Sep 1945, Seibert 2145 (US). **San Martin:** Schunke 4843 [in fruit] (F, US); Mariscal Caceres, Tocache Nuevo, Quebrada de Huaguisha (margen derecha del Rio Huallaga, 400-450 m, 3 Jul 1974, Schunke 7146 [in fruit] (F). **Ucayali:** middle Ucayali, Cashiboplaya, 10° S, 1923, Tessman 3179 (G, NY, S).

Eucharis cyaneosperma is the only species of Eucharis with blue-coated seeds. The species appears close to E. ulei, but differs by its usually shorter leaves, tube morphology, irregularly dentate to quadrate staminal cup (Fig 16A), and seed color. Eucharis cyaneosperma also occupies more upland sites than is usually characteristic of E. ulei. The species is nowhere abundant throughout its broad range. Collections are concentrated in the southern end of the range of E. cyaneosperma, while E. ulei is more common to the north (Fig. 10). The two species may represent sibling, allopatric divergences from a common ancestor that have since come into secondary contact.

9. EUCHARIS LEHMANII Regel (Figs. 17D-F), insertae sedis.

Gartenfl. 38: 313-314, t. 1300, Fig. 1. 1888. TYPE: ex hort, from bulbs collected by Lehmann near Popayan, Colombia, Apr 1888, Regel s. n. (holotype (fragmentary): LE; photo of holotype: FLAS!, K!). Urceolina lehmannii (Regel) Traub. Pl. Life 27: 57-59. 1971.

Bulb subglobose, not seen. Leaves 2; petiole 45.5 cm long, 3.5 mm thick; lamina ovate-elliptic, 24-25 cm long, 16 cm wide, short acuminate, basally subcordate and attenuate to the petiole. Scape not seen; bracts lanceolate; bracteoles linear-lanceolate. Flowers 4; pedicels to 30 mm long; limb patent, spreading to ca. 4 cm; tube ca. 25 mm long, ca. 1.2 mm wide below, dilating abruptly to 8 mm at the throat; outer tepals 20-22 mm long, 8-10 mm wide, ovate-lanceolate, acute-apiculate; inner tepals 18-20 mm long, 10-12 mm wide, obtuse. Staminal cup 7-8 mm long (to apex of tooth), deeply cleft between each stamen to < 2 mm from the throat; each stamen bidentate, the teeth long-lanceolate, equaling the free filament in length; free filament linear, 7-8 mm long, ca. 1 mm wide; anthers sub-basifixed, versatile. Style

slightly exerted beyond the anthers. Ovary globose-ellipsoid, ca. 6 mm long, ca. 4 mm wide; ovules ca. 10 per locule. Fruit and seed unknown.

DISTRIBUTION AND ECOLOGY: Extremely rare in the understory of moist, lower montane forest of the Cordillera Oriental in Cauca Department of Colombia (Fig. 18), 1200 m.

ADDITIONAL MATERIAL EXAMINED: COLOMBIA. Cauca: Aganche, Río Orejas, 1200 m, Lehmann 5883 (K).

Eucharis lehmanni is known only from the fragmentary type (a single flower), and a single specimen at Kew with only one flower present. A Ecuadorean specimen mislabeled as the type of E. lehmannii, received from Kew (Lehmann 7775), turned out to be E. astrophiala (Ravenna) Ravenna. The novel morphology of the staminal cup (Fig. 17E), somewhat analagous to the androecium of Caliphruria hartwegiana and C. tenera, and its distribution above 1000 m, suggests that E. lehmanni may be a peripheral isolate of subg. Eucharis, with novel morphological character states that frustrate the determination of its phylogenetic relationships. An alternative hypothesis is that E. lehmannii is a relict taxon with characters of intermediacy between Eucharis and Caliphruria. Phylogenetic analysis (see Chapter XI) places this species in a rather isolated position between the relict taxa comprising paraphyletic subg. Heterocharis and a monophyletic clade comprising Caliphruria and Urecolina. The best evidence of its systematic position is the figure accompanying Regel's (1888) description. The plant figured, in morphology and habit of the flower, resembles Eucharis subg. Eucharis. Given the paucity of material available, I would retain E. lehmannii in subg. Eucharis with the designation incertae sedis to indicate the uncertainty of the systematic position of this species. In 1984, I was

not able to successfully collect this species at the locality of Lehmann 5883 in Colombia, an area now largely deforested.

10. EUCHARIS CORYNANDRA (Ravenna) Ravenna (Figs. 17G-I).

Phytologia 57: 95-96. 1985. Urceolina corynandra Ravenna. Pl. Life 34: 80-81. 1978. TYPE: Peru, Cajamarca, Chinganza, between Aramango and Montenegro, 2 Jul 1973, Ravenna 2090 (holotype: herb. Ravenna; isotypes: K!, NY, MO ex TRA).

Bulb globose, 47 mm long, 37 mm diam; tunics light brown. Leaves elliptic lanceolate; petiole 25-27 cm long, 3.5-5 mm thick; lamina 20-27 cm long, 5 cm wide, apically acute. Scape 50 cm tall, slender, ca. 2 mm diam distally; bracts lanceolate, ca. 32 mm long. Flowers 8-10; pedicels 15-23 mm long, thin; perianth tube curved, 17-18 mm long, ca. 1 mm wide for most of its length, abruptly dilated to 3-4 mm at the throat; limb spreading to 3-4 cm wide; outer tepals 27-29 mm long, 6-7 mm wide, ovate-lanceolate, acute-apiculate at the apex; inner tepals ca. 28 mm long, 8-10 mm wide; ovate, acute. Staminal cup short, funnelform, thick and waxy in texture, 3.5 mm long, 7.5 mm wide, with two obtuse teeth between each free filament, somewhat plicate; free filaments club-shaped, appearing narrowly elliptic-lanceolate when dry, ca. 6.2 mm long, 1.8 mm wide, abruptly dilated to ca. 1 mm at the base, inserted adaxially between two of the teeth; anthers oblong-linear, ca. 3 mm long, versatile, black, [densely pubescent according to Ravenna (1978)]. Style 30-44.5 mm long, stigma tri-lobed. Ovary globose-ellipsoid, 6 mm long, 3 mm wide; ovules 4-6 per locule, superposed. Fruit and seed unknown.

DISTRIBUTION AND ECOLOGY: Known only from the type locality (Fig. 18), in tropical forest on slopes, near a small ravine with



Dieffenbachia sp., Heliconia sp., Clusia sp. and Xyphidium coeruleum Aubl. Elevation not reported.

Eucharis corynandra in size and number of the flowers, as well as ovule number, shows affinity to both E. castelnaeana (Baillon) Macbr. and E. plicata Meerow. The short staminal cup and distinctive club-shaped free filaments (Fig. 17H) are the principal unique characters of this species. I cannot, however, confirm Ravenna's (1978) description of the anthers as densely pubescent. Though no elevation data were supplied by the author, it is likely an upland isolate from the Amazonian center of the subgenus, having colonized the lower limits of the "ceja de montaña" forest formations in Cajamarca department of Peru.

11. EUCHARIS OXYANDRA (Ravenna) Ravenna (Fig 17A-C). Phytologia 57: 95-96. 1985. Urceolina oxyandra Ravenna. Wrightia 7: 251-253. 1983. TYPE: **Peru**: Huanuco, Huanuco, Rio Chinchao, below Carpish on rd to Tingo Maria, 1800 m, 19 Jul 1964, Hutchison et al. 5983 [specimens prepared from bulbs flowered in cultivation at UC, 26 Apr 1967]. (holotype: USM; isotypes: MO ex TRA!, UC!).

Bulb not seen. Leaves (one seen) elliptic; petiole 17 cm long, 4-6 mm thick; lamina 25 cm long, 12 cm wide. Scape 27-28 cm tall; bracts 34-35 mm long, ovate-lanceolate. Flowers 6-7, (crateriform?), cernuous; pedicels ca. 19 mm long; tube curved, 25 mm long, 1.5 mm diam below, dilated abruptly at the throat to 3.5 mm; tepals spreading to 27 mm wide; outer series 17-19 mm long, 6.7 mm wide, ovate-lanceolate, acute-apiculate; inner series 17-18 mm long, 8-9 mm wide, ovate, obtuse. Staminal cup very short, 0.8-1.5 mm long, 3-3.5 mm wide, edentate or with two obtuse teeth between the free filaments; free filaments ca. 7 mm long, ca. 1 mm wide at the base, narrowly subulate; anthers oblong,



3.3 mm long, sub-basifixed, eventually versatile; pollen grain ca. 42.36  $\mu\text{m}$  polar diam, ca. 68.36  $\mu\text{m}$  longest equatorial diam. Style 32.8 mm long; stigma 2-2.5 mm wide. Ovary globose-ellipsoid, 6 mm long, 4 mm wide; ovules 6-8 per locule. Fruit and seed unknown.

DISTRIBUTION AND ECOLOGY: Eucharis oxyandra is not known in the wild state. The collector's field notes (UC) indicate that three bulbs were found at the type locality (Fig. 18) "exposed on surface of ground with evidence of past cultivation, in deep shade near abandoned hut above road. The third bulb proved to be Urceolina urceolata (R. & P.) M. L. Green."

This unusual species has the smallest staminal cup of any Peruvian Eucharis of subg. Eucharis (Fig 17B). The long, almost linear, free filaments are another unusual feature of the androecium. The polymorphism of the staminal cup (both edentate and obtusely dentate forms represented in the isotypes, Fig. 17B) is puzzling, and adds further credence to my suggestion that this character has been over-weighted as an indicator of species delimitation in the alpha-taxonomic literature relating to the genus. Alternatively, it is possible that the two bulbs found by the collector and representing this species were of two different origins.

In publishing Urceolina oxyandra, Ravenna (1983) was apparently unaware of the unusual situation in which the species was found, having examined only a duplicate at USM which seems to have lacked the detailed field notes of the collector. He argued that the unusual morphology of the androecium (reduced staminal cup; long, narrowly subulate filaments), similar to that of Urceolina, supported the inclusion of Eucharis within Urceolina (Traub, 1971), a position he recently reversed

(Ravenna, 1985). This type of androecial morphology is characteristic of two putative intergeneric hybrids between Eucharis and Urceolina, X Urceocharis edentata Wright and X U. clibranii Masters.

Given that the plant was discovered as an apparent artifact of cultivation in company with a bulb of Urceolina, and in a geographic area of loose sympatry for the two genera, I thought it possible that E. oxyandra might represent a hybrid between Eucharis and Urceolina. X U. edentata was supposedly collected in the wild in Peru (Wright, 1910). Pollen of E. oxyandra, however, stains 100% with Alexander's (1969) stain. Both X U. edentata and X U. clibranii produced very little pollen (Wright, 1910), an observation confirmed when I examined specimens of both hybrids. The morphology of the perianth, at least as it appears in dried material, to some degree resembles the campanulate flowers of the two X Urceocharis hybrids. Pollen grain size of the species is more like that of Eucharis subg. Eucharis, but exine sculpturing (Fig. 12 in Chapter V) resembles that of Urceolina. Fertile intergeneric hybrids are not unknown in Amaryllidaceae; hybrids of Amaryllis belladonna L. and Brunsvigia Heist. are known to be fertile (Traub, 1982).

Alternatively, E. oxyandra might be a relict taxon close to the ancestor of Urceolina, a genus whose divergence from Eucharis may have been relatively recent (see Chapter XI). Phylogenetic analysis (Chapter XI) supports this latter hypothesis. The northern half of Peru is a center of pancratioid diversity, rich in small genera with novel and sometimes intermediate morphological characters (Meerow, 1985; MS in prep.). At present, it seems best to treat E. oxyandra as a species of Eucharis, even though its shared characteristics with Eucharis are

symplesiomorphous. Its cladistic relationships are obscured by the large amount of unknown character state data (Chapter XI). As in E. astrophiala, E. corynandra, and E. lehmannii, this species exhibits a pattern of morphological novelty characteristic of peripheral isolation in Eucharis. Similarities to other subgenera or genera are likely the result of canalized development (Stebbins, 1974), a reoccurring pattern within and among the tribes of "infrafamily" Pancratioidinae (Meerow, 1985).

I currently have seedlings of a putative cross of Urceolina microcrater and a Peruvian Eucharis species in cultivation. When these plants flower, the status of E. oxyandra may need reappraisal.

## 12. EUCHARIS PLICATA Meerow (Fig. 19).

Bulb subglobose, 5-6 cm long, 4 cm wide, tunics brown. Leaves 2-4 at anthesis, petiole 25-35 cm long; lamina widely elliptic to ovate, (19-) 20-30 (-35) cm long, 7-12 (-14) cm wide, short acuminate, very shortly attenuate to the petiole, thin, lustrous dark green adaxially, silvery-green abaxially, abaxial cuticle densely striate. Scape 40-60 cm tall; bracts 29-30 mm long, ovate-lanceolate; bracteoles successively shorter and narrower. Flowers (7-) 9-10, sometimes lightly fragrant; pedicel sub-erect, 10-15 (-25) mm long; perianth tube 25-28 mm long, 2.5-3 mm wide throughout most of its length, dilating abruptly to 6-10 mm at the throat; limb spreading to 30-40 mm; tepals ovate, recurved at the apex, subequal; outer series ca. 19-24 mm long, 9-14 mm wide, apiculate; inner series 16-23 mm long, 11-15.5 mm wide, apically acute. Staminal cup campanulate, ca. 8.5-12 mm long (to apex of teeth), 10-12 (-15) mm wide, apically white, basally pale greenish-yellow, plicately folded on either side of the filamental trace, bidentate; each stamen 4.5-5.5 mm

wide, the anther-bearing part subulate, 2-3.5 mm long, apically obtuse, anthers oblong-linear, sub-basifixed, erect at first then becoming versatile, grayish brown, 3.5-4 mm long; pollen grain 41.3-43.5  $\mu$ m polar diam, 59.9-68.9  $\mu$ m longest equatorial diam. Style 36-40 mm long; stigma ca. 2.5 mm wide. Ovary globose-ellipsoid, green, ca. 5-6 mm long, 3.4-4 mm wide; ovules 4-8 per locule. Capsule ca. 1 cm long, 2 cm wide; seeds 1-2 per locule, ca. 1 cm long, 5 mm wide; testa shiny black.  $2n = 46$ .

Key to the subspecies of E. plicata:

1. Flowers not noticeably fragrant; perianth tube dilating to 6-7.5 mm at the throat; staminal cup deeply plicate, ca. 12 mm long to apex of teeth; teeth longer than subulate portion of filament, coarsely serrulate, imbricate; style reaching to half the length of the cup; ovules 7-8 per locule ..... 12a. subsp. plicata
1. Flowers mildly fragrant; perianth tube dilating to 7.5-10 mm at the throat; staminal cup only shallowly plicate, ca. 8-10 mm long to apex of teeth; teeth shorter than subulate portion of filament, entire, non-imbricate; style reaching to just below the teeth; ovules 4-5(-7) per locule ..... 12b. subsp. brevidentata

12a. E. plicata subsp. plicata (Fig. 19). Brittonia 36: 18-25.

1984. TYPE: Peru, San Martín, Mariscal Cáceres, Tocache Nuevo, Quebrada de Huaguisha, right bank río Huallaga opposite Tocache Nuevo, 8°09'S lat, 76°27'W long, 500-600m, 14 Dec 1981, Plowman et al. 11394 (HOLOTYPE: FLAS!; ISOTYPES: F, K, NY, USM).

Flowers without noticeable fragrance; pedicel sub-erect, 10-15 mm long; perianth tube 22-24 mm long, dilating abruptly to 6-7.5 mm wide at the throat; outer tepals 18-23 mm long, 9-12 mm wide; inner tepals 16-20

mm long, 11-12 mm wide. Staminal cup ca. 12 mm long and wide, deeply plicate on either side of the filamental trace; the anther-bearing portion of each filament inserted between 2 irregular, obtuse, coarsely serrulate teeth each 4-5 mm long, adjacent pairs somewhat imbricate and appearing as one; pollen grain ca. 43.45  $\mu$ m polar diam, ca. 68.9  $\mu$ m longest equatorial diam. Style reaching to 1/2 the length of the staminal cup. Ovules 7-8 per locule.

DISTRIBUTION AND ECOLOGY: Known only from the type locality where it is locally abundant (Fig. 18). This population appears to have hybridized with E. ulei, and contains a range of intermediate morphs, all showing reduced pollen stainability, and the occasional presence of non-homologous chromosomes. It is unclear whether these represent a highly variable F1, the F2, or the results of introgression with E. plicata subsp. plicata.

ADDITIONAL MATERIAL EXAMINED: PERU. **San Martin:** same locality as the type, 16 Jul 1982, Meerow et al. 1025 (FLAS); same locality as the type, 4 Aug 1974, Schunke 8046 (F).

PUTATIVE HYBRIDS WITH E. ULEI: PERU. **San Martin:** same locality as the type, 16 Jul 1982, Meerow et al. 1030, 1031 (FLAS).

13b. E. plicata subsp. brevidentata Meerow, var. nov.

Subspecies nova differt a subspecies typica dentibus staminalibus brevioribus et non serrulatis vel imbricatis. TYPE: Bolivia, no collection information, ex hort Fairchild Tropical Garden from collections by Fred Fuchs Jr., 3 Oct 1984, Meerow 1143 (FLAS!).

Flowers mildly fragrant; perianth tube 25-29 mm long, dilating abruptly to 7.5-10 mm wide at the throat; outer tepals 20-24 mm long, 9-12 mm wide; inner tepals 18.7-23 mm long, 12-15 mm wide. Staminal cup



8-11 mm long (to apex of teeth), 10.5-14 mm wide, only shallowly plicate; teeth ca. 1.5-2 mm long, reaching to about half the length of the subulate portion of the filament, obtuse, entire, non-imbricate; pollen grain ca. 41.3  $\mu$ m polar diam, ca. 59.9  $\mu$ m longest equatorial diam. Style reaching to just below the apex of the teeth. Ovules 4-6(-8) per locule.

ETYMOLOGY: The epithet of this subspecies refers to the short teeth of the staminal cup.

DISTRIBUTION AND ECOLOGY: Rare in the understory of pre- and lower montane rain forest of north-central Peru and Bolivia (Fig. 18), 200-420 m; flowering August-October.

ADDITIONAL MATERIAL EXAMINED: PERU. **Amazonas:** Río Cenepa, 10-12 km NW of Huampami, ca. 420 m, 2 Oct 1972, Berlin 148 (NY); Río Cenepa, vicinity of Huampami, ca. 5 km e of Chávez Valdavia, Quebrada Huampami, ca. 78° 30' W, 4° 30' S, 200-250 m, 15 Aug 1978, Kujikat 365 (MO).

Eucharis plicata is closest to E. castelnaeana and may represent an upland segregate of the latter taxon. The phenetic relationship between the two species is most evident in E. plicata subsp. brevidentata, which in characteristics of the staminal cup and ovule number is intermediate between subsp. plicata and E. castelnaeana. From the latter E. plicata may be distinguished by its wider leaves and tepals, larger flowers, absence of any noticeable floral fragrance, campanulate staminal cup which is plicate along the filamental traces (Fig 19), more numerous ovules, and fruit and seed morphology typical of subg. Eucharis. Eucharis castelnaeana and E. plicata may represent the fragmentation of a more widespread ancestral taxon during the Pleistocene (see Chapter IX for discussion). Such a putative ancestor



may have resembled var. brevidentata, which has the most "generalized" morphology (cf. other Amazonian species of subg. Eucharis) of the three taxa. The disjunct distribution of known populations of subsp. brevidentata, to both the north and south of the distributions of subsp. plicata and E. castelnaeana, lends further credence to this hypothesis. The results of cladistic analysis (see Chapter XI) support this hypothesis.

13. EUCHARIS CASTELNAEANA (Baillon) Macbride (Fig. 20). Publ. Field Mus. Nat. Hist. Bot. Ser. 11: 47. 1931. Caliphruria castelnaeana Baillon. Bull. Mens. Soc. Linn. Paris 144: 1133-1136. 1894. TYPE: Peru, Ucayali, Pampa del Sacramento, Jun 1847, Castelnau s.n. (holotype: not located; isotype: P!). Urceolina castelnaeana (Baillon) Traub. Pl. Life 27: 57-59. 1971.

Eucharis narcissiflora Huber. Bol. Mus. Goeldi Para 4: 543. 1906. TYPE: Peru, Ucayali, Sarayacu, Catalina, 25 Jun 1898, Huber 1574 (holotype: MG!; isotype [photo and fragment]: F!). Urceolina narcissiflora (Huber) Traub. Pl. Life 27: 57-59. 1971.

Plant to 4-5 dm tall. Bulb small, sub-globose, 2.2-3 (-4.5) cm long, 1.4-2.7 cm wide; neck 1-2 cm long, 1-1.5 cm wide; tunics tannish brown. Leaves 2-4; petiole (10-) 13-17 (-25) cm long, 3-6 cm wide; lamina narrowly ovate-elliptic, (10-) 15-20 cm long, 5-7 (-10) cm wide, apex shortly acuminate, lustrous dark green adaxially, lighter green abaxially, margins undulate. Scape (2.5-) 3-4 (-5) dm tall, 5-6 mm diam proximally, ca. 3 mm diam distally; bracts (2.5-) 3-4 cm long, ovate-lanceolate, greenish-white. Flowers (7) 8-10, pendent, small, with a faint, lemon fragrance; pedicels 10-18 mm long; tube 15-25 (-30) mm long, 1-1.5 (-2) mm wide for most of its length, abruptly dilated near

the throat to 5-6 (-8) mm wide; tepals patent, spreading to (2.5-) 3-4 cm, often distally recurved, sometimes strongly reflexed for their entire length; outer tepals (ovate-) lanceolate, 15-20 mm long, 5-7 mm wide, apiculate; inner tepals ovate, 11.5-18.7 mm long, 8-11 mm wide, acute. Staminal cup funnelform-cylindrical to cylindrical, usually sub-cylindrical proximally and abruptly dilated at 1/2-2/3 of its length, (5.5-) 7-8 (-9.5) mm long (to apex of tooth), (7-) 9-11 (-12) mm wide, zoned greenish-yellow in the proximal 1/3-2/3, slightly incurved at the rim, waxy and slightly succulent in texture, bidentate between each free filament, conspicuously plicate between the teeth, very shallowly cleft between each tooth (< 1 mm) and as deep or more deeply cleft between the teeth and the free filament (> 1 mm); teeth 0.5-1 mm long, reaching to about half the length of the free filaments, obtuse, entire; free filament subulate, (1.5-) 2-3 (-4) mm long, 1.5-1.5 mm wide at the base, obtuse or acute; anthers 3-4.5 mm long, oblong, greyish-brown, sub-basifixed, more or less versatile at anthesis; pollen grain ca. 39.45  $\mu\text{m}$  polar diam, ca. 55.8  $\mu\text{m}$  longest equatorial diam. Style 25-35 mm long, reaching the apex of the cup or slightly inserted; stigma ca. 1.5 mm wide. Ovary globose, 3.5-5 mm diam, white to greenish-white; ovules (2-) 4-5 (-7) per locule. Capsule sub-globose, shallowly trilobed, ca. 1 cm long, 1.5 cm wide, glaucous green, thin-walled, sometimes abscising indehiscently; seeds 1-3 per locule, compressed-ellipsoid, ca. 1 cm long, 5 mm wide; testa dull black, rugose.  $2n = 46$ .

DISTRIBUTION AND ECOLOGY: Understory of lowland and premontane, often seasonally inundated, primary rain forest in the Amazon basin, most commonly in Peru, rare in Colombia and Brazil (Fig. 18), 100-200 m,

flowering June-September(-December). Vernacular names: amangay, sacha cebolla.

ADDITIONAL MATERIAL EXAMINED: BRAZIL. **Amazonas:** Rio Juruá, Rio Miry, Jul 1901, Ule 5737 in part (MG). COLOMBIA. **Amazonas:** vicinity Leticia, ex hort Fairchild Tropical Garden from collections made by R. Buttons, 1 Apr 1984, Watson 1868 (FLAS). PERU. **Loreto:** Isla Santa María, near Yurimaguas, Huallaga Valley, 150-200 m, 16 Sep 1948, Ferreyra 4984 (MO); Maynas, Quebrad Sucusari, Llachapa camp of Explorama, north side of Rio Napo below Mazan, forest on somewhat sandy lateritic soil, 140 m, 6 Nov 1979, Gentry et al. 27569 (MO); Maynas, Yanamono, Explorama Tourist camp on Rio Amazonas between Indiana and mouth of Rio Napo, 72° 48' W, 3° 28' S, seasonally inundated tahuampa, 120 m, 28 Jul 1980, Gentry et al. 29203 (MO); Puerto Arturo, lower Rio Huallaga below Yurimaguas, ca. 135 m, 24-25 Aug 1929, Killip & Smith 27801 (NY, US); same locality as preceding, Aug 1929, Killip & Smith 27844 (F, NY, US); between Yurimaguas and Balsapuerto (lower Rio Huallaga basin), 135-150 m, 26-31 Aug 1929, Killip & Smith 28249 (US); Santa Rosa, lower Rio Huallaga below Yurimaguas, ca. 135 m, Killip & Smith 28886 (F, NY, US); Maynas, Santa María de Nanay, Colonia San Francisco de Indies Yaguas, 1.5 km del Fundo Balcón Momon, 106-110 m, 15 Nov 1984, Schunke 14154a (FLAS); Alto Amazonas, Yurimaguas, Camino a "Schunguyce" al sur este de Puerto Arturo, near Yurimaguas, 150-200 m, 1 Dec 1984, Schunke 14156 (BM, COL, F, FLAS, G, GB, GH, K, MO, NY, P, S, UC, US); Pebas on the Amazon, 30 Jul 1929 Williams 1898 (F, S, US); lower Rio Huallaga, Sapotoyacu, Santa Rosa, 155-210 m, 11 Nov 1929, Williams 4906 [n fruit] (F); Puerto Arturo, Yurimaguas, lower Rio Huallaga, 155-210 m, 15 Nov 1929, Williams 5051 (F).

Eucharis castelnaeana is most common in the vicinity of Yurimaguas in Peru (Fig. 18), and is sometimes locally abundant in rain forest understory. It has the smallest flowers of any species in subg.

Eucharis. It is the major exception to the correlation of reduced flower size with loss of fragrance which otherwise characterizes

Eucharis. Several living collections produce a mild, lemon scent when ambient temperatures are high (as does E. plicata var. brevidentata).

It is the only species of subg. Eucharis in which the ripe capsule is not leathery and orange in color. The glaucous, green, thin-walled capsule is tardily dehiscent, and may abscise without opening, though the seeds within are fully ripe. The infructescence tends to bend to the ground, as is common among some Crinum species (Hannibal, 1972). In this manner an indehiscent fruit may rot, thus facilitating dispersal. The seeds of this species are also unusual in that the testa is dull brownish-black and rugose. The seeds are not as turgid as most Eucharis, and are wedge-shaped from compression in the capsule. They appear to contain less endosperm than typical seeds of subg. Eucharis, resembling seeds of some Pancratium species.

Eucharis castelnaeana appears to be autogamous. It is the only species of Eucharis that successfully sets fruit with self-pollen. Unmanipulated inflorescences regularly set 50-75% of their capsules.

Eucharis castelnaeana exhibits some degree of variability in flower size (Fig. 20A), and androecial morphology. In his relatively undetailed description of E. narcissiflora, Huber (1906) made no reference to E. castelnaeana, even though it was described from nearly the same location as the former. The two taxa represent the extremes of floral size diversity of a single species. Populations represented by

Schunke 14154a (Fig. 20Ai) have flowers almost twice as large as those of Schunke 14156 (Fig. 20Aii), but are otherwise indistinguishable. Shape of the staminal cup in the latter collection can range from nearly cylindrical to funnelform-cylindrical.

Eucharis plicata is the closest species to E. castelnaeana, both in phenetic distance and phylogenetically. It is very likely that both species share immediate common ancestry. Both E. corynandra and E. oxyandra may represent peripheral isolates of this same ancestral complex. Both latter species are known only from lower to mid-montane sites of the "ceja de montana" zone in Peru.

Baillon (1894) considered E. castelnaeana intermediate between Caliphruria and Eucharis in his argument for combining these two genera. Baillon probably weighed flower size heavily in his judgement, one of only two characters by which E. castelnaeana resembles Caliphruria. In Baillon's time, most other small flowered Eucharis were not yet described. The green, thin-walled capsule of E. castelnaeana is also like the fruit of Caliphruria. Baillon (1894) gives no indication whether he was familiar with the fruit of either Eucharis or Caliphruria. Nonetheless, perianth and pollen exine morphology place E. castelnaeana squarely in E. subg. Eucharis, despite its aberrant fruit and seed morphology.

## 2. EUCHARIS subg. HETEROCHARIS Meerow, subg. nov.

Subgenus Eucharis affinis a qua imprimis differt floribus plerumque non pendulis, tubo perianthii bene infra fauce dilato, limbo plerumque minus expanso, ovario grandius et ovulis numerosis en quoque loculo. TYPE SPECIES: Eucharis X grandiflora Planchon and Linden, Fl. Serres Jard. Eur. Ser. I, 9:255. 1853.



Large bulbous perennial herbs. Leaves petiolate, persistent; lamina ovate, thin, plicate or more or less smooth between the veins, undulate margined, apically acuminate, subcordate basally and shortly attenuate to the petiole, bright or dark green adaxially, light green abaxially, the abaxial epidermal cells variably striate; petiole subterete. Inflorescence scapose, umbellate, terminated by two green ovate-lanceolate bracts. Flowers sub-sessile or shortly pedicellate, 2-7, white, 7-8 cm long, strongly fragrant, declinate (rarely subpendulous), funnelform-campanulate (rarely crateriform); perianth tube cylindrical to subcylindrical below, abruptly dilated at one third to one half of its length, curved, tinged green below; limb of six ovate tepals in two series, imbricate for half their length, subequal, spreading somewhat above, often slightly undulate. Stamens basally connate into short or long staminal cup partially adnate to the upper portion of the tube, striped green or yellow within along the filamental traces, variously toothed or edentate; distal portion of the filaments linear or subulate, sometimes incurved; anthers linear, versatile at anthesis; pollen grain 40-60  $\mu\text{m}$  (polar axis), 60-76  $\mu\text{m}$  (longest equatorial axis), the exine coarsely reticulate. Style filiform, well-exserted beyond the staminal cup and slightly assurgent; stigma deeply trilobed, often green. Ovary large, ellipsoid, trigonous, appearing rostellate when dry; ovules usually 16-20 per locule, ellipsoid, biseriate. Capsule green, seeds blackish-brown with a slightly rugose testa (E. anomala). 3 species and 2 natural hybrids in Western Colombia, Ecuador and rarely Peru.



Key to the species and hybrids of subg. Heterocharis:

1. Leaves deeply plicate; staminal cup reduced to a basal connation of the filaments less than 5 mm long
  2. Staminal cup acutely bidentate between each filament, teeth ca. 2 mm long ..... 1. E. X grandiflora
  2. Staminal cup edentate or rarely with a single obscure tooth less than 1 mm long at the base of one or several stamens.
    3. Perianth tube markedly curved, cylindrical for 1/2-2/3 of its length, then abruptly dilated distally to the throat; free filament somewhat incurved; stigmatic papillae unicellular ..... 2. E. sanderi
    3. Perianth tube straight or only slightly cernuous, sub-cylindrical proximally but distally dilating gradually towards the throat; free filament straight; stigmatic papillae multi-cellular ..... 3. X Calicharis butcheri
1. Leaves relatively non-plicate; staminal cup well-developed, greater than 1 cm long.
  4. Leaf length-to-width ratio usually equal to or less than 2; perianth more or less campanulate, tepals spreading only 45-60° from the throat; staminal cup acutely bidentate, strongly recurved at the margin; ovules 16-20 per locule; plants of Ecuador, very rare in Peru ..... 4. E. anomala
  4. Leaf length-to-width ratio usually greater than 2; perianth crateriform, tepals spreading ca. 90° from the throat; staminal cup obtusely bidentate to quadrate, not strongly recurved at the margin; ovules 9-12 per locule; plants of the Huallaga valley in Peru ..... 5. E. amazonica

1. *EUCHARIS X GRANDIFLORA* Planchon and Linden (Figs. 25A-C). Fl. des Serres Jard. Eur. Ser. 1, 9: 255. 1853. LECTOTYPE: Fl. des Serres Jard. Eur. Ser 1, 9: pl. 957. Urceolina grandiflora (Planchon & Linden) Traub. Pl. Life 27: 57-59. 1971.

Eucharis mastersii Baker. Curtis' Bot. Mag. t. 6831. 1885. TYPE: ex hort Sander (holotype, K!; photo, F!). Urceolina mastersii (Baker) Traub. Pl. Life 27: 57-59. 1971.

Eucharis lowii Baker, Gard. Chron. 13:538-539, 1883. TYPE: ex hort Low (holotype, K!; photo, F!). Urceolina lowii (Baker) Traub. Pl. Life 27: 57-59. 1971,

Bulb 3-5 cm diam, neck 2-4 cm long, tunics light brown. Leaves 1-3; petiole 19-36 mm long, 5-7 mm thick; lamina ovate or elliptic, 20-33 cm long, (10-) 13-16 cm wide, apically acuminate, sub-cordate basally and shortly attenuate to the petiole, deeply plicate, adaxial surface lustrous dark or bright green, abaxial surface light green and densely striate, margins undulate. Scape 4-5 dm tall, 5-6 mm diam, subterete; bracts ovate-lanceolate, green at first, soon marcescent, 2.5-4.8 cm long, 14-17 mm wide. Flowers 2-6, funnelform-campanulate, declinate, sweetly fragrant; pedicel short, 5-7 (-10) mm long, 2.5-3.4 mm diam; tube curved, 40-55 mm long, 1.5-2 mm wide below, dilating at 1/2 to 1/3 its length to 20-25 mm at the throat, green in the proximal half, white distally; tepals ovate, imbricate for half their length, white, margins usually undulate, spreading slightly apically; outer series (30-) 35-40 mm long, (18-) 20-26 mm wide, acute-apiculate; inner series 25-35 (-40) mm long, 23-31 mm wide, obtuse. Staminal cup short, 5-7.5 mm long (to tooth), 23-25 mm wide, stained green or yellow where adnate to the dilated portion of the tube, with 2 acute or obtuse teeth between each

stamen, teeth ca. 1.5 mm long; stamens (5-) 6.7-7.5 (-10) wide at the base from tooth to tooth, free filament 7-8.5 (-10) mm long, linear or narrowly subulate, 1-1.5 mm wide at the base; anthers oblong-linear, 5.5-6.7 (-7.5) mm long, slightly curved; pollen with only 10% stainability. Style filiform, (67-) 74-85 mm long, green, assurgent, well-exserted beyond the stamens, stigma deeply 3-lobed, 2.5-3.5 (-5) mm wide, white or greenish. Ovary oblong, rostellate, 12-19 mm long, 6-8 mm wide; ovules 16-20 per locule, globose, superposed. Fruit and seed unknown, doubtfully ever formed.

DISTRIBUTION AND ECOLOGY: Rare in the understory of primary and secondary rainforest of southern Chocó and northwestern El Valle departments of Colombia (Fig. 22), 80-600(-1000) m elevation, but widely cultivated throughout western Colombia below 1750 m. Introduced and persisting in Ecuador. The plant appears to be functionally sterile. Most collections are from cultivation, and putatively native populations may be remnants of cultivation.

ADDITIONAL MATERIAL EXAMINED: COLOMBIA. **Chocó:** entre Istmina y Condoto, Río San Juan y Río Iró, 80-100 m, 5 Aug 1944, Garcia-Barriga 11525 (COL, US); **El Valle de Cauca:** Río Cabrera, Tambi, Río Sumapaz, Cundinamarca, 600-1000 m, Feb 1883, Lehmann 2644 (K); Cordova, Río Dagua, Lehmann 2736 (K in part); Río Teta, Cauca Valley, 1000 m, Lehmann 7776 (F, GH, K, NY, US); Cauca, 1000 m, Lehmann s.n. (K); 50 km SE of Buenaventura on old road to Pacific coast, Río Anchicaya, 500 m, 22 Jul 1984, Meerow & Teets 1127 (FLAS). ECUADOR. **Carchi:** Chical, path from Juan Maldonado to Tobar Danuso, flowered in cultivation, 23 Dec 1982, Madison et al. s.n. (SEL). **Guayas:** Guayaquil, cultivated, Nov 1925,

Mille 40 (QCA). Los Rios: Hacienda Ana María, Canton Vinces, 60 m, Y. Mexia 6644 (GH, US); vicinity Durán, cultivated, Rose & Rose 23627 (US).

Eucharis X grandiflora has had an unfortunate nomenclatural history, having long been confused with E. amazonica Lind. ex Planch. (Meerow and Dehgan, 1984). Meerow and Dehgan (1984) re-established E. grandiflora (without hybrid designation) as a species distinct from E. amazonica in Eucharis subg. Heterocharis. At the time, I considered E. lowii and E. mastersii to be distinct, but closely related to E. X. grandiflora. In 1984, I collected material in Colombia referable to E. lowii Baker, and received living material of E. mastersii collected in Ecuador. Baker (1893) described both species from cultivated material. According to Baker, E. lowii had a staminal cup half as long as that of E. "grandiflora." He was probably refering to E. amazonica or E. anomala (as E. grandiflora var. moorei Baker). When I compared the staminal cup of E. lowii to that of the lectotype of E. X grandiflora, the synonymy of E. lowii with E. X grandiflora became evident. In all respects, the two plants seemed identical. Baker considered E. lowii a hybrid of E. mastersii and E. "grandiflora." He also considered E. mastersii Baker (1885) to be a hybrid between E. sanderi and E. "grandiflora." Baker distinguished E. lowii from his earlier taxon E. mastersii merely by its slightly longer-exserted staminal cup, a difference that does not hold up to scrutiny. I now believe that both E. mastersii and E. lowii are elements of a slightly variable hybrid taxon, E. X grandiflora, a putative hybrid of E. sanderi and E. anomala. Though never collected in western Colombia, E. anomala does occur in contiguous northwestern Ecuador. Therefore, it was likely a collection of this hybrid which Planchon and Linden (1853) described as E.

grandiflora. Eucharis X grandiflora appears intermediate in all respects to E. anomala and E. sanderi. Virtually all collections of E. X grandiflora are from cultivated populations in Colombia and Ecuador. Pollen stainability of either Colombian or Ecuadorean collections of E. X grandiflora is never better than 10%, and I have not succeeded in obtaining seeds in cultivation with either sibling pollen or pollen of other species. The hybrid is, however, slightly variable in leaf morphology, number of flowers, and color of androecial pigmentation throughout its range, the extremes of which were recognized respectively as E. mastersii (Fig. 26A) and E. lowii (Figs. 26B-C) by Baker (1885, 1893). This may be the consequence of two or more hybridization events involving the same parents, or, more likely, the result of selective propagation of a variable F1 through human agency.

2. EUCHARIS SANDERI Baker (Fig. 23). Curtis' Bot. Mag. t.6676. 1883. TYPE: ex hort (K!). Urceolina sanderi (Baker) Traub. Pl. Life 27: 57-59. 1971.

Bulb 42.5-49 mm long, 32-47 mm wide; neck thick, 24-30 mm wide; tunics light brown. Leaves petiolate, persistent; petiole 31-50 cm long, 5.5-6 (-8) mm thick; lamina ovate or elliptic, (23-) 30-37 cm long, (10-) 14-17 cm wide, thin, deeply plicate between the veins, undulate margined, apically acuminate, subcordate basally and shortly attenuate to the petiole, bright green adaxially, light green abaxially, the abaxial surface intensely striate. Scape subterete, 45-54 cm long, 5-6 mm diam; bracts lanceolate, 45-65 (-77) mm long. Flowers 2 (-3), sub-sessile (pedicels 5 mm or less long), strongly fragrant, declinate, funnelform-campanulate; perianth tube (45-) 50-60 (-70) mm long, cylindrical to subcylindrical and 2-3 mm wide below, abruptly dilated at



1/2 of its length to 20-27 mm wide, curved, tinged green proximally; tepals white, ovate, subequal, imbricate for half their length, spreading somewhat distally; outer series 26-32 (-37) mm long, 16-20 mm wide, apiculate; inner series 24-30 (-33) mm long, 20-25 mm wide.

Stamens basally connate into a short staminal cup partially adnate to the upper portion of the tube, ca. 20-24 mm wide, striped green within along the filamental traces, only shortly exerted beyond the rim of the throat, edentate or rarely with one to few obscure teeth; free filaments (6-) 7-9 (-9.7) mm long, 1.8-2.2 mm wide at the base, linear, incurved; anthers (5.6-) 6-8 (-9) mm long linear, versatile, often curved; pollen grain 40-60  $\mu$ m (polar axis), 50-70  $\mu$ m (longest equatorial axis), the exine mostly coarsely reticulate. Style filiform, (66-) 75-80 (-90) mm long, well exerted beyond the staminal cup and slightly assurgent, white, sometimes flushed green; stigma deeply and obtusely trilobed, (2.8-) 3-4 mm wide. Ovary large, ellipsoid, trigonous, appearing rostellate when dry, (10-) 15-20 mm long, (5-) 7-9 (-11) mm wide; ovules (7-) 10-20 per locule, ellipsoid, biseriate. Fruit and seed imperfectly known, capsule becoming at least 5 cm long and 3.3 cm wide, seeds several per locule.

DISTRIBUTION AND ECOLOGY: Endemic to western Colombia, occurring locally on sites with rich soil in the understory of wet, lowland rainforest, primarily in Chocó Dept. (Fig. 22), frequently along watercourses; occasional in similar habitats in El Valle de Cauca Dept., (5-) 30-300 (-1000) m. Collections above 500 m elevation in the Río Cauca Valley (Von Sneider 404, 1129, & 5208) may be adventive. Flowering may occur at any time of the year.



ADDITIONAL SPECIMENS EXAMINED: COLOMBIA. **Chocó:** headwaters of Río Tutunendo, east of Quibdó, 20-21 May 1931, Archer 2197 (US); Río San Juan between Dipurdu & San Miguel, ca. 100 m, 14 Aug 1976, Gentry & Fallon 17687 (MO); Corcovada region, upper Río San Juan, Yeraquí valley, 200-275 m, 24-25 Apr 1939, Killip 35276 (US); Andagoya, 70-100 m, Apr 1939, Killip 35401 (US). **El Valle de Cauca:** Río Calima, La Trojita, 5-50 m, 19 Feb-10 Mar 1944, Cuatrecasas 16380 (F); Río Calima, Quebrada de La Brea, 30-50 m, 18-22 May 1946, Cuatrecasas 21195 (F); Río Telembi, 12 Aug 1880, Lehmann 65 (G); Río Dagua, 0-300 m, 11 Aug 1884, Lehmann s.n. (G). **Cauca:** El Tambo, La Costa, 1000 m, 3 Jul 1935, von Sneider 404 (S); El Tambo, 800 m, 7 Jul 1936, von Sneider 1129 (S). **Caldas:** Riseralda [?], Tatama, Santa Cecilia [La Celia?], 800 m, 1 Dec 1945, von Sneider 5208 (S).

This species is denoted by its large, sweetly fragrant funnelform-campanulate flowers, large ovary and capsule, and reduced staminal cup. The narrow distribution of E. sanderi suggests it evolved within the confines of the wet Pacific rainforests of Colombia, conceivably from a fragment population of an ancestral taxon isolated during the Pliocene uplift of the Andes (see Chapter XI). Natural hybrids exist between E. sanderi and both E. anomala (E. X grandiflora) and Caliphruria subedentata (X Calicharis butcheri). A single collection (Cuatrecasas 16380) in which maturing capsules are represented suggests that E. sanderi produces the largest fruit in the genus. Despite the many putatively primitive characteristics of E. sanderi (e.g., large flowers, strong fragrance) in common with E. anomala, ovule number of E. sanderi is considerably variable, and its leaves are deeply plicate. The

reduced morphology of the androecium is, however, the major advanced character of E. sanderi.

3. X CALICHARIS BUTCHERI (Traub) Meerow, nothogen. et comb. nov. (Figs. 22D-E). Eucharis butcheri Traub. Pl. Life 23: 68, 1967. TYPE: ex hort Traub, purported to have been collected in Panama by J. N. Giridlian, Traub 1051 (holotype: MO ex TRA!). Urceolina butcheri (Traub) Traub. Pl. Life 27: 57-59. 1971.

Eucharis sanderi Baker var. multiflora Baker, Curtis' Bot. Mag. t.6831, 1885. TYPE: Lehmann s.n. (holotype: K!). Eucharis sanderi Baker subsp. multiflora (Baker) Traub. Pl. Life 23: 65. Urceolina sanderi subsp. multiflora (Baker) Traub. Pl. Life 27: 57-59. 1971.

Bulb 6-7 cm long, 3.8-5 cm wide, neck short and thick, tunics brown. Leaves 2-3; petiole 20-40 cm long, 5-6 mm wide; lamina elliptic, 21-26 (-35) cm long, (10.5-) 12-15 cm wide, shortly acuminate, subcordate-attenuate at the base, conspicuously plicate, adaxial surface bright to dark green, adaxial surface lighter green and intensely striate. Scape 5-6 dm long, 4-5.5 mm diam; primary bracts lanceolate, 41-57 mm long. Flowers 4-6 (-7), funnelform-campanulate, fragrant; pedicels 4.5-5 (-8) mm long; tube 35-42 mm long, funnelform proximally, dilating gradually from 1.5 mm wide at the base to 3.5 mm wide at median length, then abruptly dilated in the distal half to 13-16 mm wide at the throat, green for most of its length, the interior of the dilated also portion stained green, most prominently along the filamental traces; tepals white, imbricate for half their length, spreading eventually to 45-55 (-60) mm wide, margins non-undulate; outer series 20-28 (-35) mm long, 12-17.5 mm wide, acute-apiculate; inner series 19-27 (-32) mm long, 18-25 mm wide, obtuse. Stamens shortly connate below, edentate or

rarely with one obscure tooth between some of the filaments, white; free filament linear, straight or slightly curved apically, 6.7-8.7 mm long, 0.6-1 mm wide at the base where abruptly dilated to 2.5-3 mm; anthers (4.5-) 6 mm long, linear-oblong, greyish-brown, mostly devoid of pollen. Style 6-7 cm long, overtopping the stamens, slightly assurgent, white distally, green proximally; stigma obtusely trilobed, (2-) 2.8-3 mm wide, papillae multicellular. Ovary globose-ellipsoid, 7.7-12 (-15) mm long, (5-) 7-9 mm wide; ovules 7-10 (-12) per locule. Fruit and seed unknown, doubtfully ever formed.

DISTRIBUTION AND ECOLOGY: Rare in western Colombia, along the Río Dagua in El Valle de Cauca Dept., and the lower Cauca

ADDITIONAL MATERIAL EXAMINED: COLOMBIA. **El Valle de Cauca:** Río Dagua, 17 Mar 1883, Lehmann 2736 (BM, K); Río Dagua, 200-500 m, Lehmann 7774 (F, K in part). **Cauca:** El Tambo, La Costa, 1000 m, 24 Jun 1936, Von Sneidern 1269 (S). **Provenance unknown:** no data, Jan 1938, Cuatrecasas 1620 (F).

This putative hybrid between E. sanderi and Caliphruria subedentata was first described by Baker (1885) as Eucharis sanderi var. multiflora. It has been collected in the wild at the interface of the distributions of both parents, and at intermediate elevations. The plant produces little pollen, none of it staining with Alexander's (1969) stain. Floral morphology is intermediate between both parents, though, like C. subedentata, the stigmatic papillae are multicellular. Like other large-flowered and fragrant Eucharis, X C. butcheri has likely been cultivated and disseminated via human agency.

Eucharis anomala Meerow, sp. nov. (Figs. 24, 25A-B).

Species a E. amazonica affinis sed differt foliis plerumque minus quam 2-plo longis quam latis, limbo campanulato patente minus quam 90°, cupula staminea ad marginem plus recurvata, dentibus stamineis acutis, et ovulis in quoque loculo magis numerosis. TYPE: Ecuador, Morona-Santiago, km 145, Cuenca-Gualaquiza, 1300 m, Jul 1982, Dodson & Embree 13200 (holotype: MO!, isotype: SEL!).

Eucharis grandiflora var. moorei Baker, Gard. Chron. 4: 628, 1888.

TYPE: ex hort Glasnevin, 1888, s. n. (K!).

Bulb 6-7 cm long, 2.5-4 cm diam, tunics brown. Leaves 2-3; petiole 2-4 dm long, 5-7 mm thick, with an anomalous arc of accessory fiber bundles near the adaxial surface; lamina broadly ovate, length/width ratio less than or equal to 2, 17-30 cm long, 10-14 cm wide, apex shortly acuminate, base appearing cordate at the base, margins coarsely undulate, lustrous dark green adaxially, lighter green abaxially, abaxial cuticle mostly without striations. Scape 5-7 dm tall, terete, 7-10 mm diam proximally, ca. 5 mm diam distally; bracts ovate-lanceolate, (25-) 35-45 mm long, green. Flowers usually 4, rarely up to 7, more or less campanulate, declinate, sweetly fragrant; pedicels usually short, 3-10 (-18) mm long; tube 40-52 mm long, cylindrical and 1.7-2 mm wide proximally, abruptly dilating at about its midpoint to (15.5-) 18.5-25 mm at the throat, white except for a slight green tinge at the base; limb spreading less than 90° from the throat to ca. 70 mm wide or less; tepals ovate, the margins undulate; outer series 3.3-4 cm long; 17-22 mm wide, apiculate; inner series 2.9-3.8 cm long, 22-27 mm wide, obtuse. Staminal cup cylindrical, (8-) 10-15 (-16.4) mm long (to apex of teeth), 20-25 mm wide, strongly recurved at the margins, white

on the exterior, yellowish-green on the interior, shallowly cleft between each stamen, bidentate between each free filament, teeth acute, 2.5-3 mm long; each stamen ca. 7-8 mm wide tooth-to-tooth; free filament subulate, (5-) 6-8.5 mm long, 2 mm or less wide at the base; anthers 5.5-6.5 mm long, oblong-linear, greyish-brown; pollen grain ca. 48.6  $\mu$ m polar diam, ca. 71.2  $\mu$ m longest equatorial diam. Style 6-7 cm long; stigma 2.5-3.5 mm wide, white. Ovary ellipsoid-trigonous, (7-) 10-13 mm long, ca. 5 mm wide; ovules 16-20, biseriate. Capsule globose, ca. 1.5 cm long, 1.3 cm wide, slightly rostellate, green, slightly glaucous; seeds 1-3 per locule, compressed globose, ca. 6 mm diam, turgid, testa blackish-brown and slightly rugose.  $2n = 46$ .

ETYMOLOGY: The epithet refers to the anomalous secondary vascular bundles of the petiole, and the systematic position of this species as the most primitive in the genus.

DISTRIBUTION AND ECOLOGY: An understory plant of primary and secondary lower montane rainforest of the Ecuadorean Andes, in Morona-Santiago and Santiago-Zamora Provinces on the east slopes, and Los Rios, Cotopaxi, and contiguous Pichincha Provinces on the western declivity, (220-) 600-1200 (-1600) m (Fig. 22); rare in the lower "ceja de montaña" of Cajamarca Department, Peru. Flowering is concentrated from January-March and again from (June-) July-September.

ADDITIONAL SPECIMENS EXAMINED: ECUADOR. **Cotopaxi:** km 52-53 on rd from Quevedo to Latacunga, Río Pilalo, 800-950 m, 11 Aug 1984, Meerow & Meerow 1137 (FLAS); same locality as preceding, 13 Aug 1984, Meerow & Meerow 1141 (FLAS). **Los Rios:** km 56 Quevedo-Santo Domingo, Río Palenque Biological Station, 220 m, flowered in cultivation, Dodson 5527 (SEL). **Morona-Santiago:** 27 km SE of San Juan Bosco, 1270 m, 27 Jan 1981, Gentry



et al 30913 (MO, SEL); Indanza-Limón (General Plaza), 1300-1600 m, 23 Mar 1974, Harling & Andersson 12779 (GB); 3 km N of Tucumbatza on road Gualaquiza-Indanza, 1200 m, forest remnants, 19 Apr 1985, Harling & Andersson 24329 (GB); Río Yunganza, rd Limon-Mendez (78° 19' W, 2° 49' S), 1100 m, 23 Sep 1979, Holm-Nielsen et al 20393 & 20407 (AAU); Río Gualaquiza and Río Bomboiza, east Andes of Sigsig, 800-1200 m, Lehmann 5882 (K); 10-20 km from Gualaquiza on rd to Sigsig-Cuenca, 1300 m, 5 Aug 1984, Meerow & Meerow 1135 (FLAS). **Pichincha:** Nanegal, west slope Andes, 5000 ft, Jameson 9 (G, P). **Santiago-Zamora:** Yurupaza, 600 m, 3 Jun 1947, Harling 1407 (GB); west side Río Valladolid, 2100-2400 m, 15 Oct 1943, Steyermark 54717 (F). PERU. **Cajamarca:** Jaen, Río Tabaconas valley, 900-1000m, May 1912, Weberbauer 6251 (GH, US);

Herbarium material of E. anomala, when first received, was assigned to E. amazonica. In 1984, I collected the species on both sides of the Ecuadorean Andes. Morphological, anatomical and karyological differences between these collections and the Peruvian E. amazonica became evident. Eucharis anomala is fully fertile, diploid ( $2n = 46$ ) and of fairly wide distribution throughout Ecuador. The anomalous arc of secondary bundles that appear in petiolar transverse sections of E. anomala, and reduced, in E. amazonica, are not found in any other species of the genus investigated. Eucharis anomala is putatively the most primitive species of the genus, and shares numerous plesiomorphic character states with other genera of "infracfamily" Pancratioidinae (e.g. large, fragrant flower, short pedicels, and numerous ovules per locule). Perianth and ovary morphology of E. anomala is similar to that of E. sanderi, but the species has a conspicuous, long-exserted staminal cup as is characteristic of subg.



Eucharis. The species also occupies a geographical position intermediate between E. sanderi (endemic to Chocó Department, Colombia) and the vast majority of subg. Eucharis. Species of subg. Eucharis are exceedingly rare on the western slopes of the Andes (Meerow, 1986). Eucharis anomala is the only species in the genus that occurs on both sides of the Andes.

The presence of E. anomala in northwestern Ecuador, and the existence of putative natural hybrids between it and E. sanderi (E. X grandiflora), might suggest that it was this plant which Planchon and Linden described as E. grandiflora. To date, however, I have not seen a single collection of E. anomala from Colombia. Furthermore, the staminal cup of the flower illustrated in the lectotype of E. X grandiflora is clearly much shorter than that of E. anomala, and the general habit of the figured plant closely resembles E. X grandiflora.

5. EUCHARIS AMAZONICA Linden ex Planchon (Figs. 25C-D). Fl. des Serres Jard. Eur. Ser. 2, 2: 1216-1217, 1857. LECTOTYPE: Fl. des Serres Jard. Eur. Ser. 2, 2: t. 1216-1217.

Bulb 3.5-6 cm diam, neck 2.8-4.5 cm long, tunics brown. Leaves usually 2-4; petiole (15-) 25-30 (-50) cm long, 5.5-9 mm thick; lamina long-elliptic, (20-) 30-40 (-50) cm long, (10-) 12-18 cm wide, length/width ratio usually greater than 2, acuminate, sub-cordate at the base and attenuate to the petiole, lustrous, dark green adaxially and shallowly or inconspicuously plicate, abaxial surface lighter green, cuticular striations obscure or largely absent, margins coarsely undulate. Scape 4.5-7 (-8) dm tall, ca. 1-1.5 cm diam proximally, ca. 5 mm diam distally, terete; primary bracts (30-) 35-58 (-61) mm long, broadly ovate-lanceolate, green. Flowers (4-) 5-6 (-8), sub-pendulous,

sweetly fragrant; pedicel (9-) 10-15 (-25) mm long; tube white throughout, curved, (41-) 46-58 mm long, cylindrical below and 2-2.5 mm wide, dilating abruptly at 1/3 length to (15-) 18-21 (-24) mm at the throat; limb white, spreading widely to 60-90 mm wide; tepals ovate, outer series 35-45 (-50) mm long, 21-30 mm wide, apiculate; inner series 30-40 (-45) mm long, 25-35 mm wide, acute. Staminal cup widely cylindrical, 11.2-13.8 mm long (to apex of teeth), (22-) 28-30 (-34) mm wide, margins slightly recurved, the interior stained green, particularly along the filamental traces, shallowly cleft between each stamen; stamens 7-8 (-9.5) mm wide at the base, each with 2 obtuse teeth, one on each side of the subulate free filament, rarely subquadrate; teeth 2-3 mm long; free filament 6.5-8 (-10) mm long, 2.8-3.4 mm wide at the base; anthers oblong-linear, 6-7 (-8) mm long, greyish; pollen ca. 51.6  $\mu$ m polar diam, ca. 78.3  $\mu$ m longest equatorial diam. Style white, 66-78 (-85) mm long, exserted 1-1.5 cm from the staminal cup, slightly assurgent; stigma deeply 3-lobed, 3-3.5 mm wide when receptive. Ovary oblong-ellipsoid, (8-) 10-14 mm long, (4-) 5-7.5 (-8) mm wide, somewhat rostellate; ovules 9-12 per locule, superposed. Fruit and seed imperfectly known, capsule reported to be green and the seed ellipsoid with a black testa (M. C. Williams, pers. comm.).  $2n = 68$ .

**DISTRIBUTION AND ECOLOGY:** An understory herb of lower and mid-montane rainforest of northeastern Peru, most prominently in the Huallaga valley in the vicinity of Moyobamba and Tarapoto (Fig. 22), 500-1500 m. Certain Peruvian populations are likely escapes from cultivation. The plant flowers at least twice per year, (May-) July-August (-September) and December-March. Widely cultivated throughout the warm tropics and as a house and greenhouse plant in the temperate

zone. Occasionally adventive in the West Indies and probably elsewhere. Vernacular names: amangais blanco, amangay, flor de cebolla, azuzena, Amazon lily, Eucharist lily.

ADDITIONAL SPECIMENS EXAMINED: PERU. **Huánuco:** Huánuco, Tingo María, 20 Aug 1940, Asplund 13214 (S); Huánuco, Tingo María, hwy La Oroya-Tingo María, Mar 1977, Boeke 1196 (NY); Leoncio Prado, Rupa Rupa, Las Palms, km 18.5 a la carretera Tingo María-Huánuco, 756-800 m, 22 Jul 1984, Schunke 14055 (F, FLAS, MO); Leoncio Prado, Rupa Rupa, Castillo Grande, al oeste de Tingo María, 24 Jul 1984, Schunke 14057 (COL, GH, F, FLAS, K, MO, NY, UC, US); Huánuco Puente Durand north of Huánuco, Río Chinchao valley, 7 Nov 1938, Stork & Horton 9880 (F, US); vicinity of Afilador, 670 m, Woytkowski 101 (F). **San Martín:** Lamas, Lamas, on trail from Tabalosos to Lams, along Río Cumbaquiri, 1/2 hour west of Río Mayo, ca. 1500 ft, 13-15 Sep 1937, Belshaw 3416 (F); near Uchiza, Huallaga valley, 500-550 m, 6 Aug 1948, Ferreyra 5154 (MO ex TRA); Zepaelacio near Moyobamba, 1200-1600 m, Mar 1934, Klug 3559 (F, G, GH, K, NY, S, NY, US); Pachiza, Río Huayabamba, 1 Aug 1959, Mathias & Taylor 3974 (F); Roque, 9 Aug 1925, Melin 92 (S); between Balsapuerto and Moyobamba, 3000 ft, Sandeman s. n. (BM); Lamas, Lamas, Fundo San Rafael, sector Santana, near Quebrada Chupishiña, 800 m, 5 Dec 1984, Schunke 14171 in part (FLAS); Moyobamba, 100[?]-1100 m, Weberbauer 4642 (G); Lamas, near Tarapoto, 840 m, Dec 1929, Williams 6348 (F, US); San Roque, 1350-1500 m, Feb 1930, Williams 7802 (F).

Eucharis amazonica was restablished as a species distinct from E. X grandiflora by Meerow and Dehgan (1984), a taxon with which it has been confused since its description by Planchon (1857). The species is indigenous only to Peru, in the upper and middle Huallaga valley, but is

grown worldwide in tropical regions and may be sporadically adventive. The species has a somatic chromosome number of  $2n = 68$ , and is at least partially sterile. No specimen of E. amazonica, in contrast to most other species, has ever been collected in fruit; pollen stainability is only 50-65%; and seed has only rarely been produced in cultivation (M. C. Williams, pers. comm. Pollen from Hippeastrum and Hymenocallis species was used; the resulting seed was inviable). It is therefore conceivable that all populations of E. amazonica constitute a single, clonal taxon. Its distribution about northeastern Peru may have been human vectored from a central parent population. I believe E. amazonica to be a triploid derived Peruvian isolate of either E. anomala or a taxon, perhaps extinct, ancestral to them both. The morphological differences between these taxa are cryptic, and virtually impossible to discern in most dried material without dissection of the ovary. Their close relationship is further supported by the presence of secondary vascular bundles in the petiole of both taxa, albeit much smaller in E. amazonica.

#### Doubtful or Excluded Names in Eucharis:

Eucharis galanthoides (Klotzsch) Linden, nomen nudum. 1862. Ann. Cat. Hort. 17: 4. This combination is based on the erroneous assumption that Linden's Eucharis galanthoides was based on Mathieua galanthoides Klotzsch (Meerow, MS in subm). No type has been located for Linden's plant, and the name E. galanthoides merely appeared as a

listing in his catalog. It is likely referable to E. castelnaeana (Baillon) Macbride.

Eucharis himeroessa Sandwith ex Standley. 1936. *Herbertia* 3: 74. This name was never validly published. It was applied to a population of E. bouchei var. bouchei Woodson & Allen from San Jose province in Costa Rica.

Eucharis paradoxa T. Moore. 1876. *Gard. Chron* 1: 242. A listed name, never validly published, applied to the plant later described as Caliphruria subedentata Baker.

CALIPHRURIA Herbert. *Edwards' Bot. Reg.* 30 (misc. no. 83): 87. 1844. Urceolina subg. Caliphruria (Herbert) Traub. *Pl. Life* 27: 57-59. 1971. TYPE SPECIES: Caliphruria hartwegiana Herbert.

Small bulbous perennial herbs. Leaves glabrous, petiolate, persistent or rarely hysteranthous; petiole subterete, distally ancipitous; lamina ovate, ovate-elliptic or elliptic, slightly succulent, apically acute or acuminate, basally attenuate to the petiole, margins non-undulate, dark green and smooth-surfaced adaxially, lighter green abaxially, the cuticle of the abaxial epidermis thickly striate or ridged, hypostomatic or with adaxial stomata only near and upon the midrib. Inflorescence scapose, umbellate; scape slender, terminating in two marcescent bracts which enclose the flowers before anthesis. Flowers pedicellate, (3-) 5-10 (-12), pedicels thin, each subtended by a linear-lanceolate bracteole, declinate or subpendulous by the laxness of the pedicel, 2-4 cm long, without noticeable fragrance, white, funnelform or funnelform-tubular, protandrous; perianth tube funnelform, dilating gradually from the base, tinged green below, or subcylindrical and white throughout, straight; limb of 6 lanceolate,



ovate or elliptic tepals in two subequal series, the segments imbricate for half their length, diverging in their distal half. Stamens connate only at the base, forming a short, membranaceous staminal cup, variously toothed or edentate between each filament, distal portion of the filament narrowly subulate or linear, subequal; anthers oblong, erect at anthesis, eventually versatile; pollen grains medium-sized (longest equatorial axis ca. 50  $\mu$ m), the exine finely reticulate. Style filiform; stigma trilobed, papillae multicellular. Ovary globose, green, with septal nectaries; ovules ellipsoid, (1) 2-7 per locule, medially superposed, placentation axile. Fruit a thin-walled, leathery, yellow-green, loculicidal capsule; seeds few per locule, globose or compressed-ellipsoid, ca. 3-5 mm long, testa black or brown.  $2n = 46$ . Four species, three endemic to western Colombia, one to Peru.

Key to the species of Caliphruria:

1. Perianth more than 2 cm long, tube more than 10 mm long.
  2. Perianth tube 9-13.5 mm long; stamens 5.8-6.8 mm long, bidentate between each, length of teeth equal to or greater than 1/2 the length of the free filament ..... 1. C. hartwegiana
  2. Perianth tube 15-25 mm long; stamens equal to or greater than 9 mm long, edentate or occasionally with 1-2 teeth between each, teeth never more than 1/10 the length of the free filament ..... 2. C. subedentata
1. Perianth equal to or less than 2 cm long, tube less than 10 mm long.
  3. Leaves hysteranthous, perianth tube funnelform, stamens less than 5 mm long, more or less fasciculate, bidentate, teeth



- much exceeding the free filament in length, free filament  
 1-2 mm long, ovules 1-2 per locule ..... 3. C. tenera  
 3. Leaves persistent; perianth tube subcylindrical; stamens 7-10  
 mm long, divergent, edentate, filaments 7-9 mm long, ovules  
 4-5 per locule ..... 4. E. korsakoffii

1. CALIPHURIA HARTWEGIANA Herbert. Edwards' Bot. Reg. 30, misc.  
 no. 83: 87. 1844. TYPE: [The species as described by Herbert from  
 Hartweg collections made near Guaduas, Colombia lacks a holotype, and I  
 have not located any specimen which could be designated as lectotype.  
 The following neotype is herein proposed]. Colombia, Huila, Rio  
 Magdalena near Paicol, 600-1200 m. Lehmann 6376 (neotype, K!).  
Eucharis hartwegiana (Herbert) Nicholson. Illus. Dict. Gard. 1884.  
Urceolina hartwegiana (Herbert) Traub. Pl. Life 27: 57-59. 1971.

Plant to 3 dm tall. Bulb globose with a brown tunic, ca. 32.8 mm  
 diam, often apically articulated into a slender neck to 19.6 mm long.  
Leaves 2-4; petiole 13 cm long, 2.5-4.4 mm thick; lamina ovate to  
 elliptic, 10-14 cm long, 3.8-6.3 cm wide, acuminate, shortly attenuate  
 to the petiole at the base. Scape 28-31 cm tall; bracts lanceolate,  
 13.5-16.8 mm long and ca. 3 mm wide at the base; inner bracteoles  
 successively smaller and narrower. Flowers 5-7; pedicels 12.8-15.8 mm  
 long, thin; perianth 19-26 mm long, white, except for the proximal 1/3-  
 1/2 of the tube which is green; tube funnelform, dilating gradually from  
 the base, 9-13.5 mm long, ca. 2-3 mm wide at the base, 5-6 mm wide at  
 the throat; limb spreading to 7.5-11 mm; tepals ovate-elliptic, the  
 outer series ca. 14.8 mm long, 3.4 mm wide, acute-apiculate, the inner  
 series ca. 12 mm long, 5 mm wide, obtuse. Stamens (Fig. 26B) 5.8-6.8  
 mm long, narrowly subulate for most of their length, dilated to ca. 2.5

mm basally where connate, bidentate between each free filament; teeth ca. 1/2 the length of the free filament; free filament ca. 1.5 mm wide at point of insertion to cup; anthers 5.2-5.4 mm long, linear, versatile. Style 25 mm long, exerted ca. 2.4 mm beyond the limb; stigma 1.8 mm wide. Ovary globose, 2.8-3.1 mm diam; ovules 2-3 per locule, axile, medially superposed; mature fruit and seed unknown.

DISTRIBUTION AND ECOLOGY: Western-central Colombia, in the understory of lower-montane forests of the Río Magdalena Valley (Fig. 27), 600-1275 m.

ADDITIONAL MATERIAL EXAMINED: COLOMBIA. Cundinamarca: Caparrapi, 1275 m., 8-13 Jun 1939, García-Barriga 7713 (COL); Ex hort: s.n. (K); 1882, s.n. (GOET). Huila: Municipio de la Plata, Vereda Agua Bonita, Finca Merenberg, 1200-1300 m, 15 Jul 1975 Díaz et al. 534 (COL).

This seldom-collected species is distinguished from C. subedentata by its smaller flowers and short stamens with long teeth interposed between the filaments (Fig. 26B). In all other respects it closely approaches C. subedentata. In view of the lack of any collections exhibiting clearcut morphological intermediacy between C. hartwegiana and C. subedentata, and their allopatric distribution, the retention of the former as a distinct species seems advisable.

2. CALIPHRURIA SUBEDENTATA Baker. Curtis' Bot. Mag. 103: t. 6289. 1877. TYPE: ex hort Beaufoy s.n. (holotype, K!; photo of type, COL!). Eucharis subedentata (Baker) Bentham and Hooker (Fig. 28). Genera Plantarum, vol. 2. 1883. Urceolina subedentata (Baker) Traub. Pl. Life 27: 57-59. 1971.

Eucharis fosteri Traub. Pl. Life 7: 36. 1951. TYPE: Colombia, Cauca, above Cali on road to Buenaventura, 2000 feet, collected by M.B.

Foster, 5 Dec 1946, Traub 17 (holotype, MO ex TRA!). Urceolina fosteri (Traub) Traub. Pl. Life 27: 57-59. 1971.

Plant to 4 dm tall, offsetting vigorously. Bulb globose-subglobose with a brown tunica, 22-45 (-63) mm long, 20-32 (-44.5) wide, often apically articulated into a slender neck 11.8-23.5 mm long and 10-15.7 mm wide. Leaves 2-4; petiole 10-28 (-37) cm long, 4-7 mm thick; lamina ovate, ovate-elliptic or elliptic, 14.5-19.5 (-21) cm long, (4.5-) 7-10 cm wide, acuminate, shortly attenuate to the petiole. Scape 25-40 cm tall, slender, 2.5-5.5 mm diam; bracts 13-25.5(-30.5) mm long, 3-5.2 mm wide at base; inner bracteoles 5-14 mm long. Flowers (3-) 5-7 (-8); pedicels (13.6-) 15.2-28 (-44.3) mm long, thin, ca. 1 mm diam; perianth (24-) 31.6-39 (-44.8) mm long, white but for the distal 1/3-1/2 of the tube which is green; tube funnelform, dilating gradually from the base, 15-25 mm long, ca. 2 mm wide at the base, 5-8 mm wide at the throat; limb spreading to 12.5-21 mm wide, tepals ovate-elliptic; outer series (15-) 17.5-22.5 mm long, 5-8 mm wide, acute-apiculate; inner series (13.5-) 15.8-20 mm long, 7-10 mm wide, obtuse-minutely apiculate. Stamens (Figs. 26C-D, 28D) less than 1 mm long, edentate, rarely with 1-2 small teeth between all or some of the filaments, white; filaments narrowly subulate-linear for most of their length, (8-) 9-11.5 (-14.6) mm long, dilating to 1.5-2.5 mm at their point of insertion; tooth, when present, 1 mm or less long; anthers (5-) 6.2-7 (-7.5) mm long, linear; pollen grain ca. 39.3  $\mu$ m polar diam, ca. 50.9  $\mu$ m longest equatorial diam. Style (28.9-) 30-40 (-45) mm long, exserted 4-6 mm beyond perianth, white; stigma 3-lobed, 1-1.5 (-2.5) mm wide. Ovary globose-ellipsoid, 3-5 mm long, 2.5-5 mm wide; ovules (2) 3-5 (-7) per locule, axile, superposed. Capsule ca. 1 cm diam; seeds 1-2 per locule,

compressed-ellipsoidal, 5-7 mm long, ca. 3-5 mm diam; testa black, rugose.

DISTRIBUTION AND ECOLOGY: Understory of lower and mid-montane forests of Western Colombia in the Cordilleras Occidental and Central, chiefly in the Río Cauca valley (Fig. 27), (760-) 1100-1800 (-2000) m.

ADDITIONAL MATERIAL EXAMINED: COLOMBIA. **Cauca:** Santander de Quilichao; selva densa en "Río Chiquito," 2000 m, 6 Oct 1954 Fernandez 2795 (COL); Río Cauca, 1400 m, Sep 1881 Lehmann 939 (BM, G); Caloto, 1200-1500m, Jun 1883 Lehmann 2885 (G); Quebrada Guatica, 1800 m, Lehmann 3269 (K); Cajamarca, Lehmann s.n. (K); Caloto, 1200-1500 m, Jun 1880 Lehmann s.n. (K); along Río La Paila above Corrinto, Central Cordillera, 1400 m, 19 Jan 1906 Pittier 1009 (US); vicinity of Medellín, Mar 23 1927 Toro 111 (NY). **El Valle de Cauca:** Río Dagua Valley, La Margarita, ca. 760 m, Apr 1939 Killip 34872 (US); "La Manuelita," Palmira, 1090-1100 m, May 1922 Pennell & Smith 6182 (US). EX HORT. Apr 3 1906, Dammer s.n. (B, GH [photo]); May 1982, Meerow 1101 (FLAS); Jun 1984, Meerow 1109 (FLAS); Jun 1984, Meerow 1123 (FLAS); ex hort Bull, s. n. (K); ex hort Linden, s. n. (K).

Caliphruria subdentata is the most common and variable species of Caliphruria, at one time found throughout the moist lower and middle montane forests of the slopes of the Cordilleras Central and Occidental west of 76° W longitude (Fig. 27), and chiefly those surrounding the Cauca Valley. As much of this forest type has been destroyed in Western Colombia, the species is no longer abundant. In the course of fieldwork in western Colombia in 1984, I was not able to find any populations of C. subdentata in either its historical localities or the remnants of lower and mid-montane forest which I explored. The species may yet

persist in more inaccessible forested sites. Living material received from Mr. Thomas Fennell was said to have been collected in Ecuador, but this information is undocumented. At present, I have seen no Ecuadorean specimens of Caliphruria, nor encountered populations in the field.

Within the range of C. subdentata, variation in leaf size, flower size, dentation of the androecium (Figs. 26C-D) and number of ovules is evident, but these patterns are, for the most part, continuous and/or mosaic in distribution, rendering recognition of subspecific taxa superfluous. The rare presence of dentation in the androecium of C. subdentata may conceivably be the result of hybridization with C. hartwegiana. The relative rarity of C. hartwegiana, and lack of living material referable to this species, precludes further analysis at this time. Though Baker (1877) characterized the species by the presence of one or two small teeth between the free filaments, the flowers present on the type specimen of C. subdentata are completely edentate.

Clonotypic material of the taxon described by Traub (1951) as E. fosteri, is distinguishable from other living material of C. subdentata only by its slightly smaller leaves and flowers.

Several letters addressed to J. G. Baker which accompanied the type specimen of C. subdentata reveal that material referable to this species was circulated, prior to its description by Baker (1877), as E. candida Planch. and Lind., the type species of Eucharis. Eucharis paradoxa, a listed name of no nomenclatural standing, was supposedly applied to plants of C. subdentata before Baker's valid publication of Caliphruria subdentata.

3. CALIPHRURIA TENERA Baker. Handbook of the Amaryllideae, p. 112. 1888. TYPE: Colombia, Río Magdalena, Aug 1844, Goudot s.n. (holotype:



K!; isotype: P!). Eucharis tenera (Baker) Traub. Pl. Life 23: 65.

1967. Urceolina tenera (Baker) Traub. Pl. Life 27: 57-59. 1971.

Plant to 2.5-3.0 dm. Bulb globose or ellipsoid, ca. 25 mm diam or 30 mm long X 17.5 mm wide, sometimes apically articulated into a short neck 10 mm long by 5 mm wide; tunica greyish brown or tan. Leaves hysteranthous, not seen. Scape, terete, slender, 16-27 cm tall, 1-2 mm diam; bracts linear-lanceolate, 17-28.3 mm long; inner bracteoles linear, the longest to 14.5 mm. Flowers 5-10; pedicels 14-23.2 mm long, thin; perianth 17-19 mm long, funnelform, white; tube 8.5-9.5 mm long, funnelform, dilating gradually from 1.3 mm wide at the base to 3-4 mm at the throat; limb spreading to 15.5 mm; tepals ovate to elliptic, the outer series 8.5-11.2 mm long, 2-2.5 mm wide, acute-apiculate; the inner series 8-10. mm long, 2.8-3.8 mm wide, obtuse. Stamens (Fig. 26A) 3-5 mm long, each stamen bidentate, 1.5-2.2 mm wide, the free filament inserted between the teeth; teeth much exceeding the free filament, 3-4 mm long; free filament 0.8-1.5 mm long, linear; anthers 4-5.5 mm long, linear; pollen grain ca. 35.2 polar diam, 53.7  $\mu$ m longest equatorial diam. Style 18-21 mm long; stigma 3-lobed, 1 mm wide. Ovary globose, 1.8-2.7 mm diam; ovules 1-2 per locule, axile, medially superposed. Fruit and seed unknown.

DISTRIBUTION AND ECOLOGY: Colombia, valley of the Río Magdalena (Fig. 27), 400 m. The hysteranthous leaves of this species suggest adaptation to drier habitats than usually characteristic of the subgenus. According to Cuatrecasas (1958), pockets of xeric vegetation do occur in the vicinity of the type locality.

ADDITIONAL MATERIAL EXAMINED: COLOMBIA. Cundinamarca [?]: "Prov. Bogota," Copó la Parada, 400m, Jul 1853 Triana 1289 (COL, US, photo GH).



Caliphruria tenera is the smallest-flowered Colombian representative of Caliphruria. It is readily distinguished by its hysteranthous leaves and the long teeth of the androecium which greatly exceed the short free filament (Fig. 26A). Unfortunately, C. tenera has not been recollected since 1853.

4. CALIPHRURIA KORSAKOFFII (Traub) Meerow, comb. nov. (Fig. 29).  
Eucharis korsakoffii Traub. Pl. Life 23: 85-87. 1967. TYPE: ex hort J. N. Giridlian from bulbs collected by Lee Moore in Peru, San Martín, Hierra waterfalls, 40 km from Moyobamba, 1500 m, Jul 16 1966, Traub 1060 (holotype: MO ex TRA!). Urceolina korsakoffii (Traub) Traub. Pl. Life 27: 57-59. 1971.

Plant offsetting weakly, to 2.5 dm tall. Bulb more or less globose, 31 mm long, 29.3 mm wide, without an appreciable neck, tunica brown. Leaves 2-4; petiole 4.5-10 cm long, 3-4 mm thick; lamina ovate-lanceolate to narrowly elliptic, 13-17 mm long, 3.3-4.8 mm wide, acute-acuminate, basally attenuate to the petiole, cuticle of the abaxial epidermis thickly ridged. Scape 15-25 cm tall, 3.5-3.7 mm diam; bracts lanceolate, 19-25 mm long, 5.5 mm wide at the base; inner bracteoles 8.5-22 mm long. Flowers 10-12, 15-20 mm long, funnelform, white, declinate to slightly ascendent; pedicels 2-4 cm long; tube subcylindrical, straight, 4-6 mm long, 2 mm wide at base, 3.2 mm wide at throat; limb spreading to ca. 2 cm; outer tepals lanceolate, 10-18.5 mm long, 4-5 mm wide, acute-apiculate; inner tepals ovate, 7.5-16 mm long, (5-) 7-8 mm wide, obtuse-minutely apiculate. Stamens (7-) 9.5-10 mm long, 0.7 mm wide at the base, edentate, diverging distally, narrowly subulate, white; anthers 3-4 mm long, oblong, dorsifixed in lower third, versatile; pollen grain ca. 32.3  $\mu$ m polar diam, 50.4  $\mu$ m longest

equatorial diam. Style 16-21 mm long, white, slightly longer than limb segments; stigma 3-lobed, (1.2-) 2.5-2.7 mm wide. Ovary globose-ellipsoid, 3.5-5 mm long, 2-3 mm wide; ovules 4-5 per locule, medially superposed. Capsule ca. 1 cm diam, yellow-green, thin-walled; seeds 1 per locule, globose, ca. 3 mm diam, testa brown.  $2n = 46$ .

DISTRIBUTION AND ECOLOGY: North-central Peru (Fig. 27) at 1500 m. Known only from the type locality in the understory of dense lower montane rainforest in humic topsoil on steep slopes, often growing wedged in the crevices of rocks.

ADDITIONAL MATERIAL EXAMINED: EX HORT. clone of type collection, s. n. (K); clonotype, Jul 1964, Traub s.n. (MO); clone of type collection, May 1982, Meerow 1096 (FLAS).

Caliphruria korsakoffii is the only species of Caliphruria presently known outside of Colombia. In the size of the flower, this species has affinity with C. tenera, but can be distinguished from the latter by its evergreen leaves, subcylindrical tube, edentate, divergent and longer stamens, pollen morphology, more numerous ovules, and altitudinal limits. The seeds of C. korsakoffii have a brown testa; those of C. subedentata are black. The ridged cuticle of the abaxial leaf surface of C. korsakoffii is quite different from the narrow cuticular striations of C. subedentata (see Chapter III). The morphological novelties exhibited by C. korsakoffii suggest a long isolation from the Colombian taxa of Caliphruria.

Figure 12.1. Staminal cup measurements used in species  
descriptions of Eucharis.

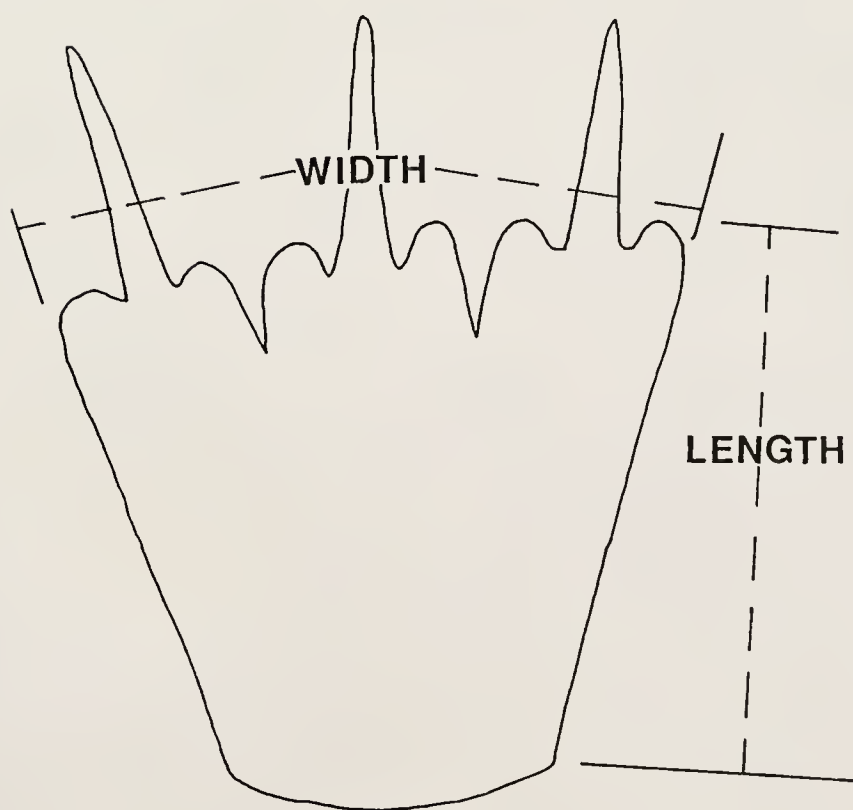
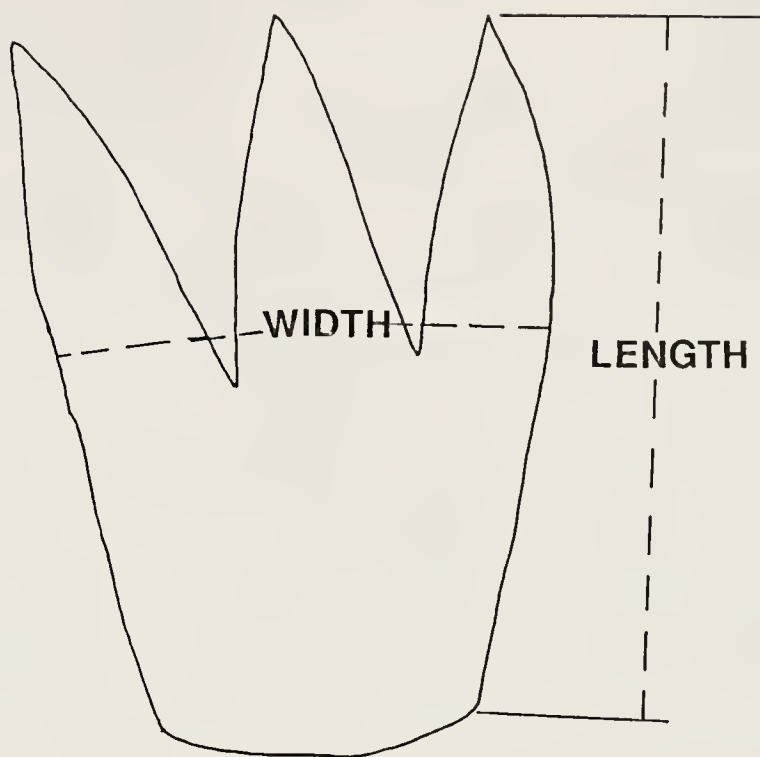


Figure 12.2. *Eucharis formosa* (Meerow 1103, FLAS) and *E. candida* (Dodson et al. 14095, SEL). A. Flowers. i. *E. formosa*. ii. *E. candida*. B. Tepals. i-ii. *E. formosa*. i. Outer tepal. ii. Inner tepal. ii-iv. *E. candida*. iii. Outer tepal. iv. Inner tepal. C. Staminal cups. i. *E. formosa*. ii. *E. candida*. D. Ovaries, longitudinal section. i. *E. formosa*. ii. *E. candida*.

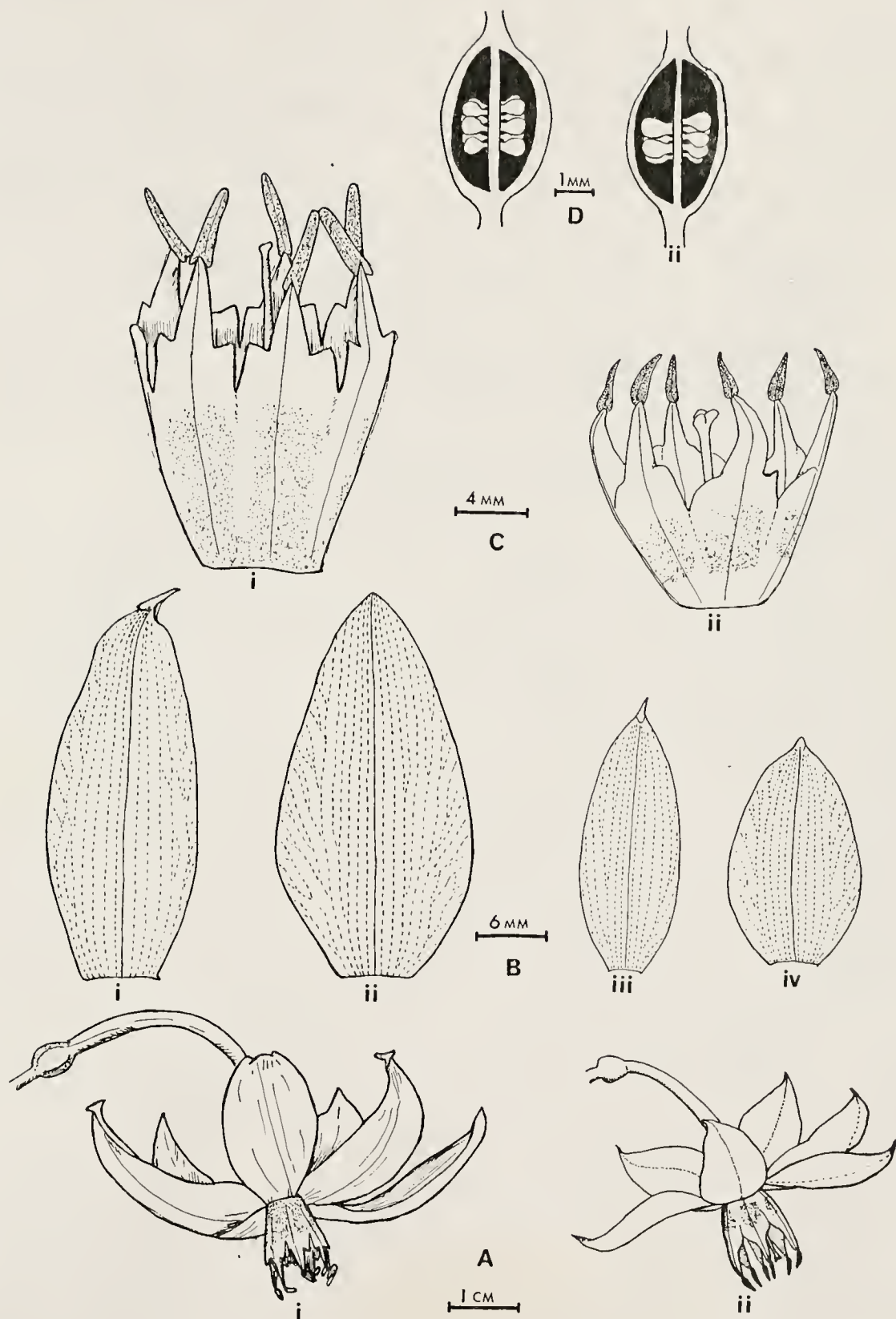




Figure 12.3. Variation in a single Peruvian population of Eucharis candida (Schunke 14155-B, FLAS).  
A. Flower with wide-spreading staminal cup. B. Flower with cylindrical staminal cup.

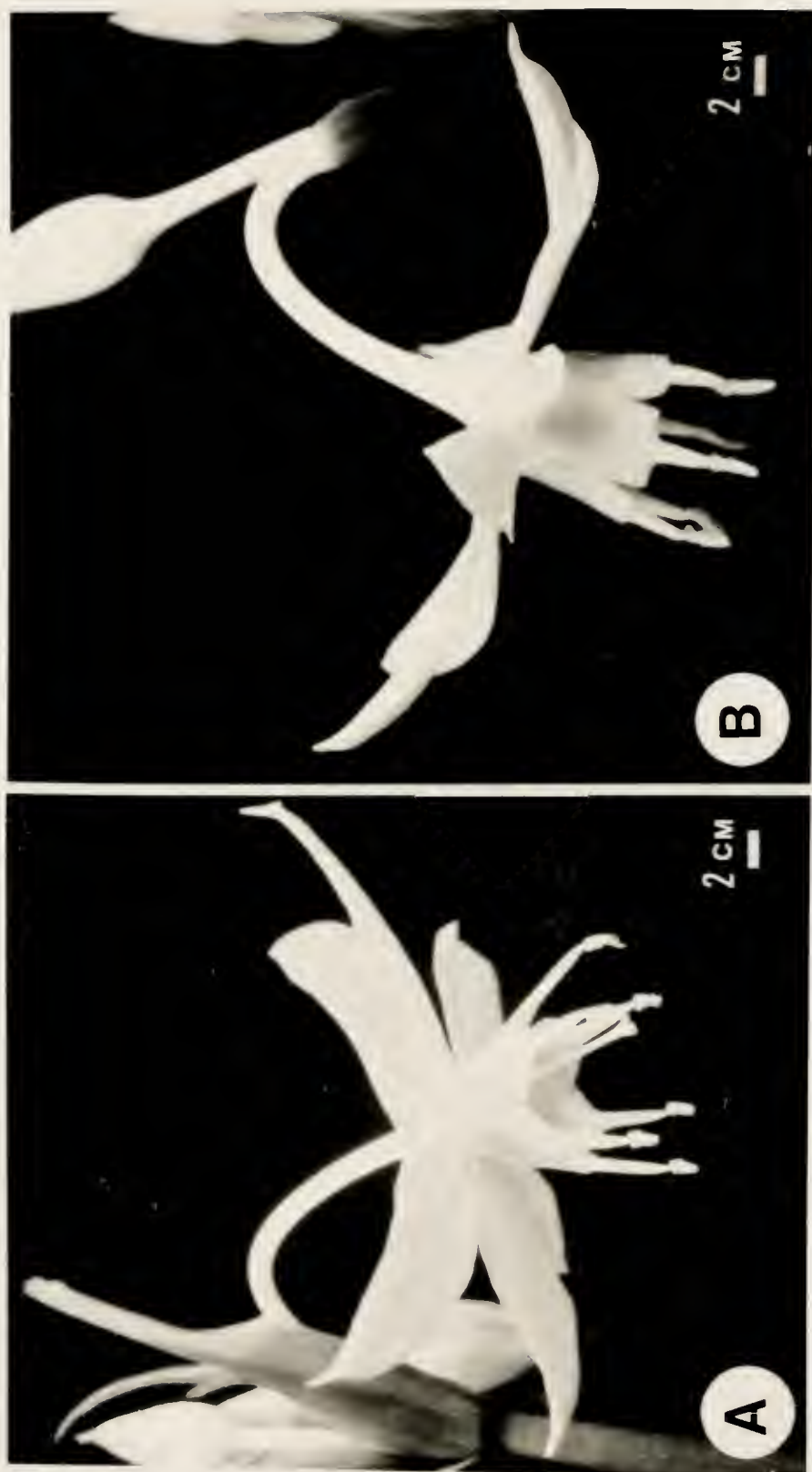


Figure 12.4. Staminal cup variation in four species of *Eucharis*.

A. E. candida. i. Besse et al. 1598, SEL. ii. Harling et al. 7400, GB. iii. Schultes & Black 8476, US. B. E. formosa. i. Penland 142, US. ii. Holguet 2655, GB. iii. Harling et al. 7201, GB. C. E. bouchei. i-ii. Variety bouchei. i. Lewis et al. 2617, MO. ii. Allen 120, US. iii. Variety dressleri (Meerow 1107, FLAS). iv. Variety darienensis (Gentry & Mori 13945, MO). D. E. ulei. i. Plowman & Kennedy 5811, GH. ii. Holotype, Ule 5737A (B). iii. Schunke 1887, F.

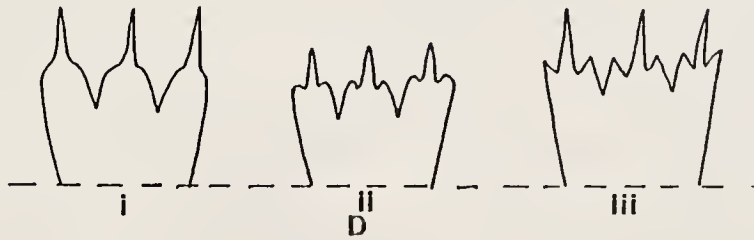
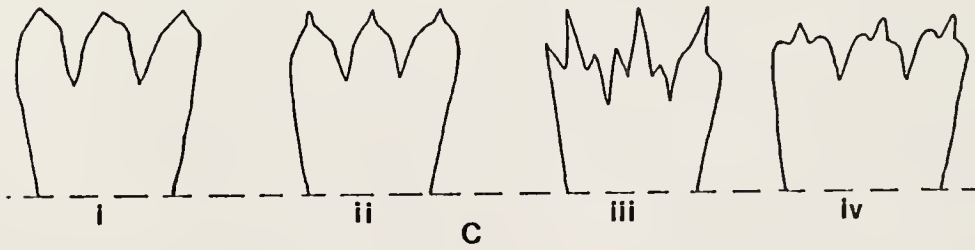
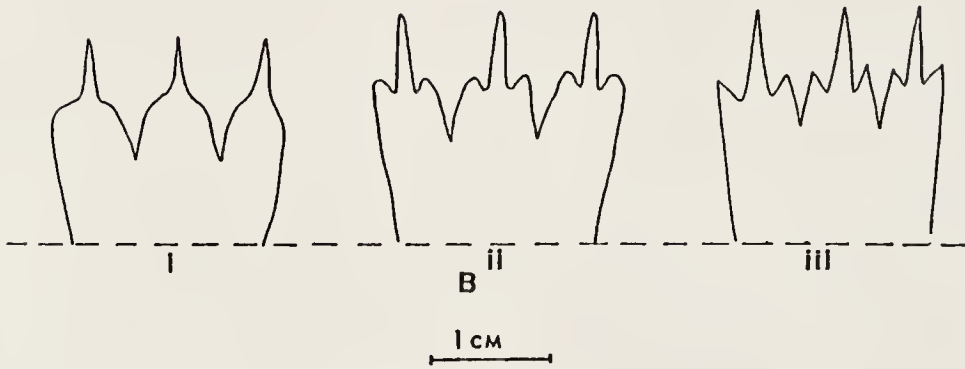
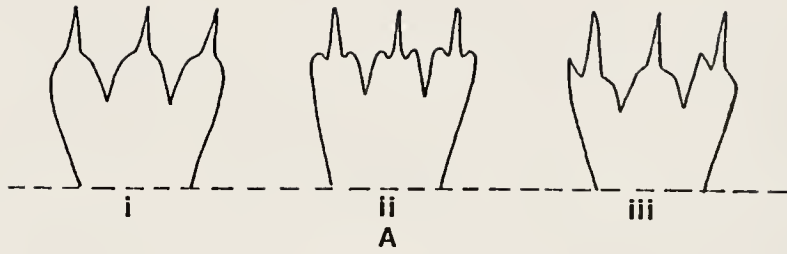


Figure 12.5. Distributions of Eucharis candida and E. formosa in  
Ecuador.

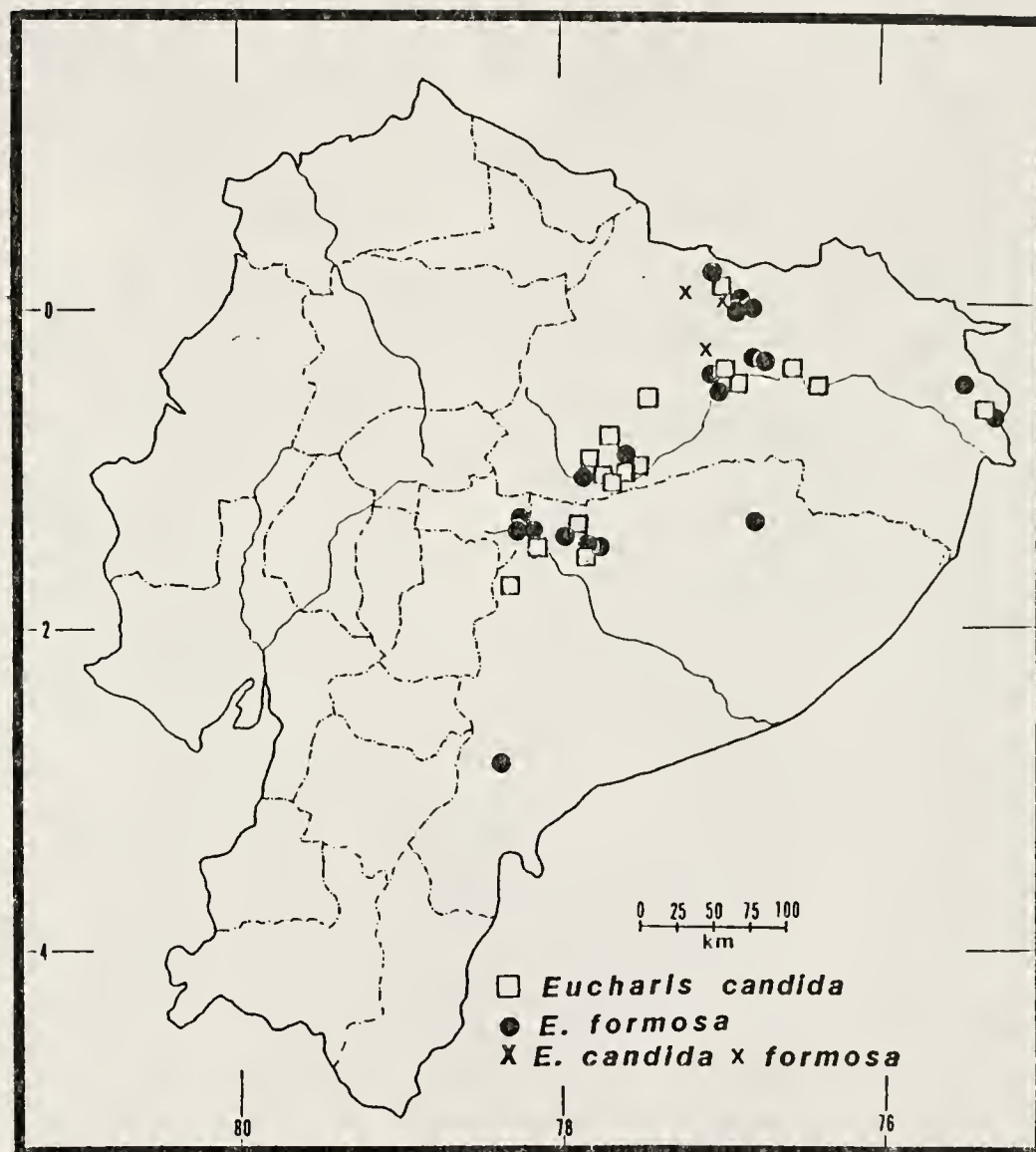




Figure 12.6. Distributions of Eucharis bakeriana, E. candida and  
E. formosa in northwestern-central South America.



Figure 12.7. Variation in *Eucharis formosa*. A-C. Meerow 1103,  
FLAS. D-E. Schunke 14171, FLAS. E. Schunke 14174, FLAS.



Figure 12.8. Eucharis bakeriana (Meerow 1108, FLAS). A. Flower.  
B. Tepals. i. Outer tepal. ii. Inner tepal. C. Staminal  
cup. D. Ovary, longitudinal section.

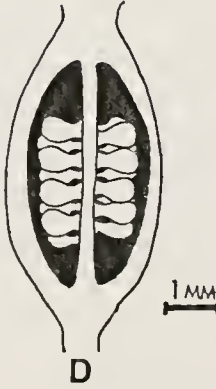
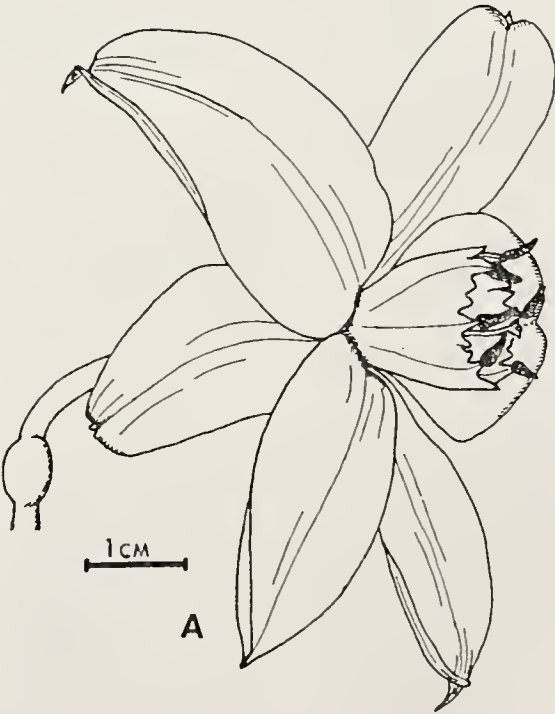
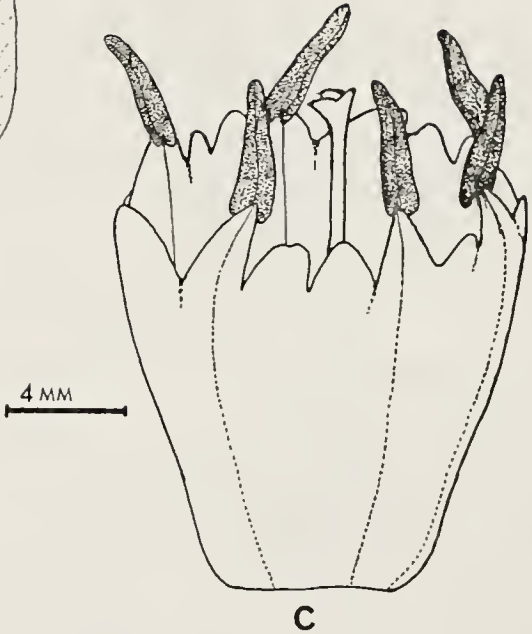
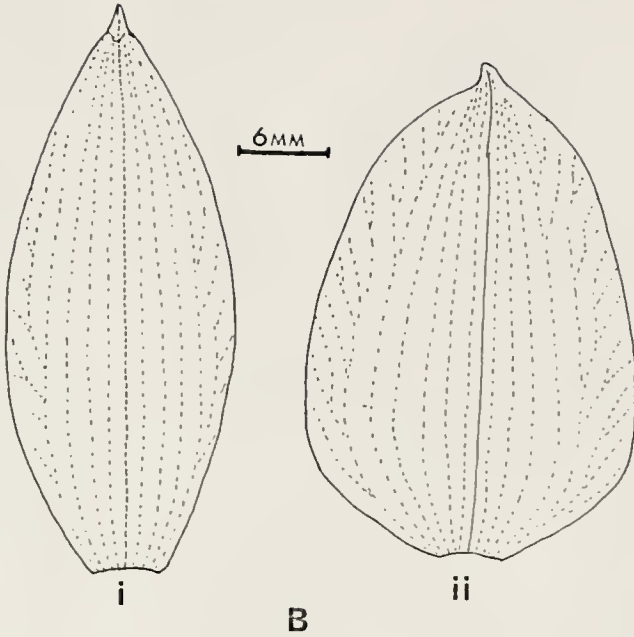




Figure 12.9. Eucharis bonplandii (Meerow 1098, FLAS).



Figure 12.10. Distributions of Eucharis bonplandii, E.  
cyaneosperma and E. ulei in northwestern-central South  
America.

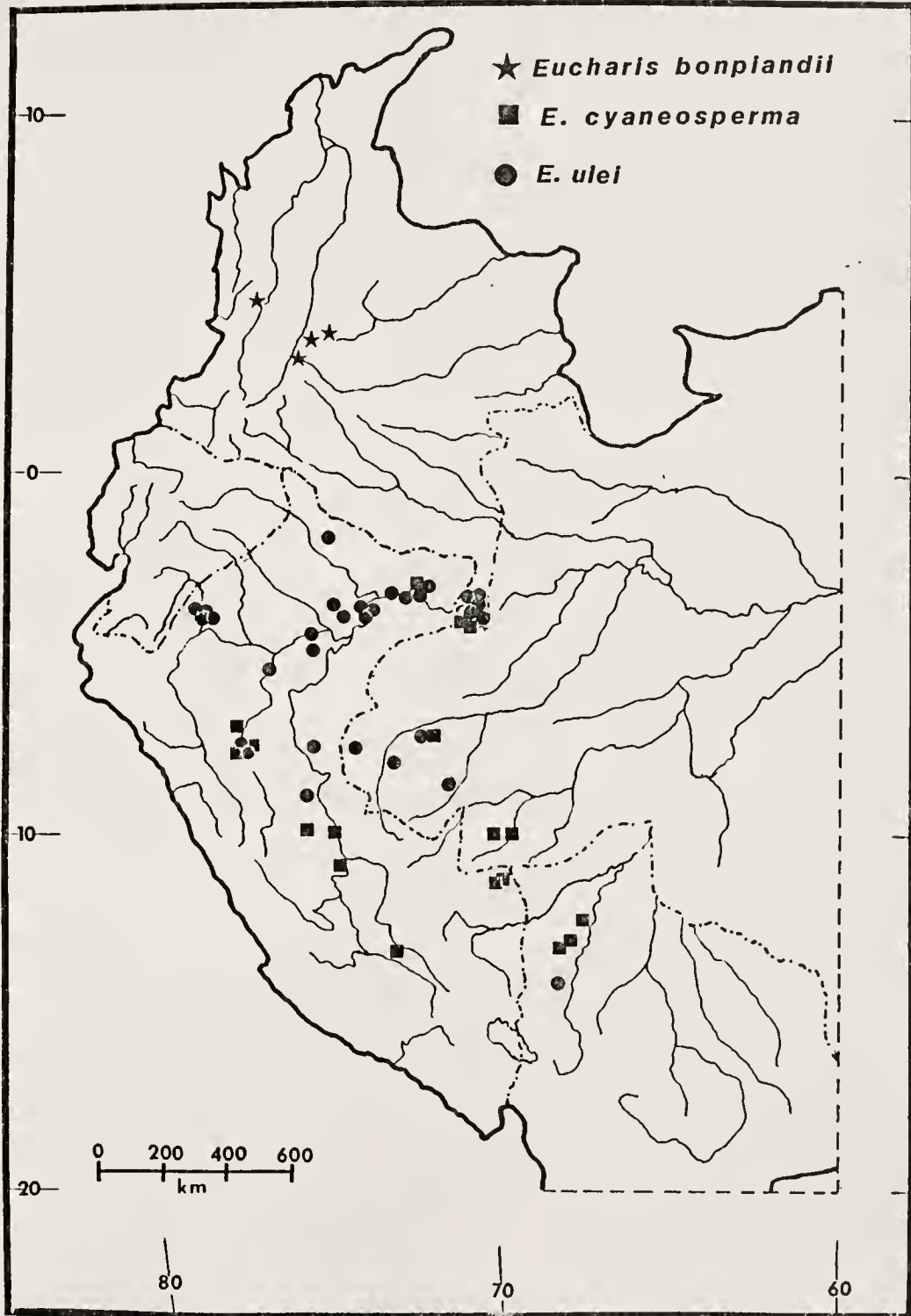


Figure 12.11. Eucharis bouchei. A. Flowers. i. Variety dressleri (holotype, Meerow 1107, FLAS). ii-iii. Variety bouchei. ii. Meerow 1125, FLAS. iii. Meerow 1157, FLAS). B. Tepals, variety bouchei. i-ii. Meerow 1125. i. Outer tepal. ii. Inner tepal. iii-iv. Meerow 1157. iii. Outer tepal. iv. Inner tepal. C. Staminal cups, variety bouchei. i. Meerow 1125. ii. Meerow 1157. D. Ovaries, variety bouchei, longitudinal section. i. Meerow 1125. ii. Meerow 1157.

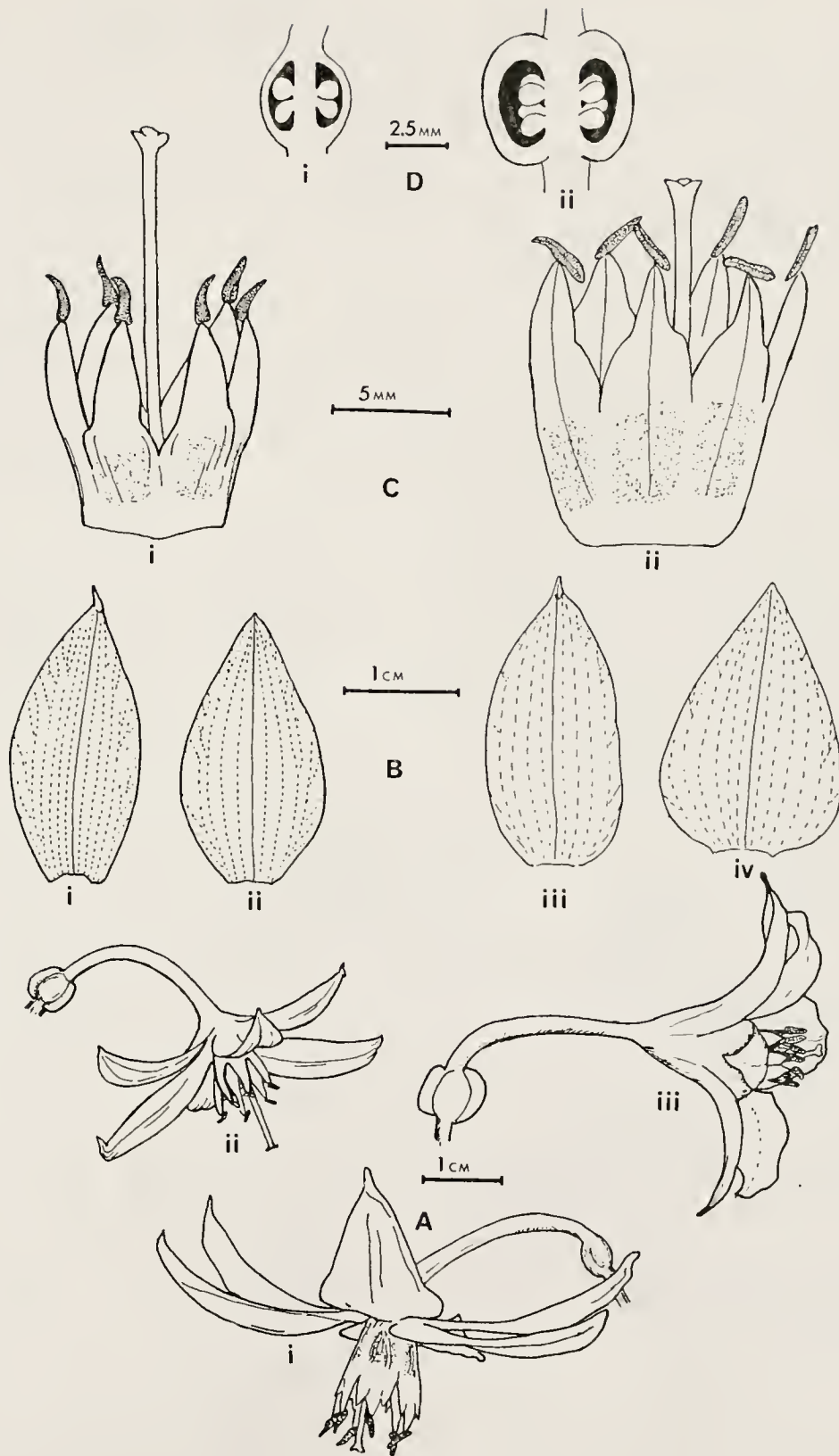




Figure 12.12. Distribution of Eucharis bouchei in Panama.

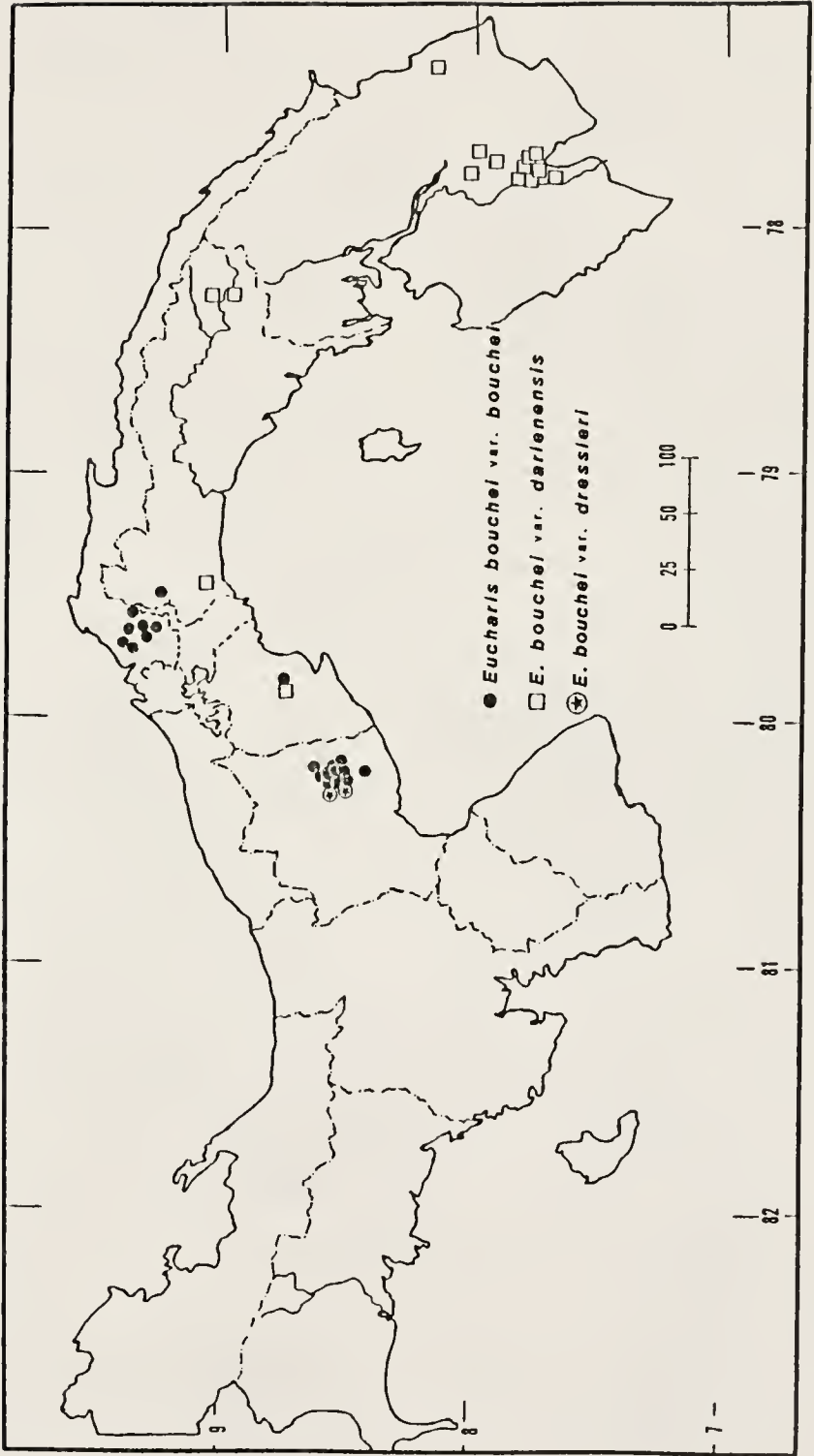


Figure 12.13. Distribution of Eucharis bouchei in Central America  
exclusive of Panama.

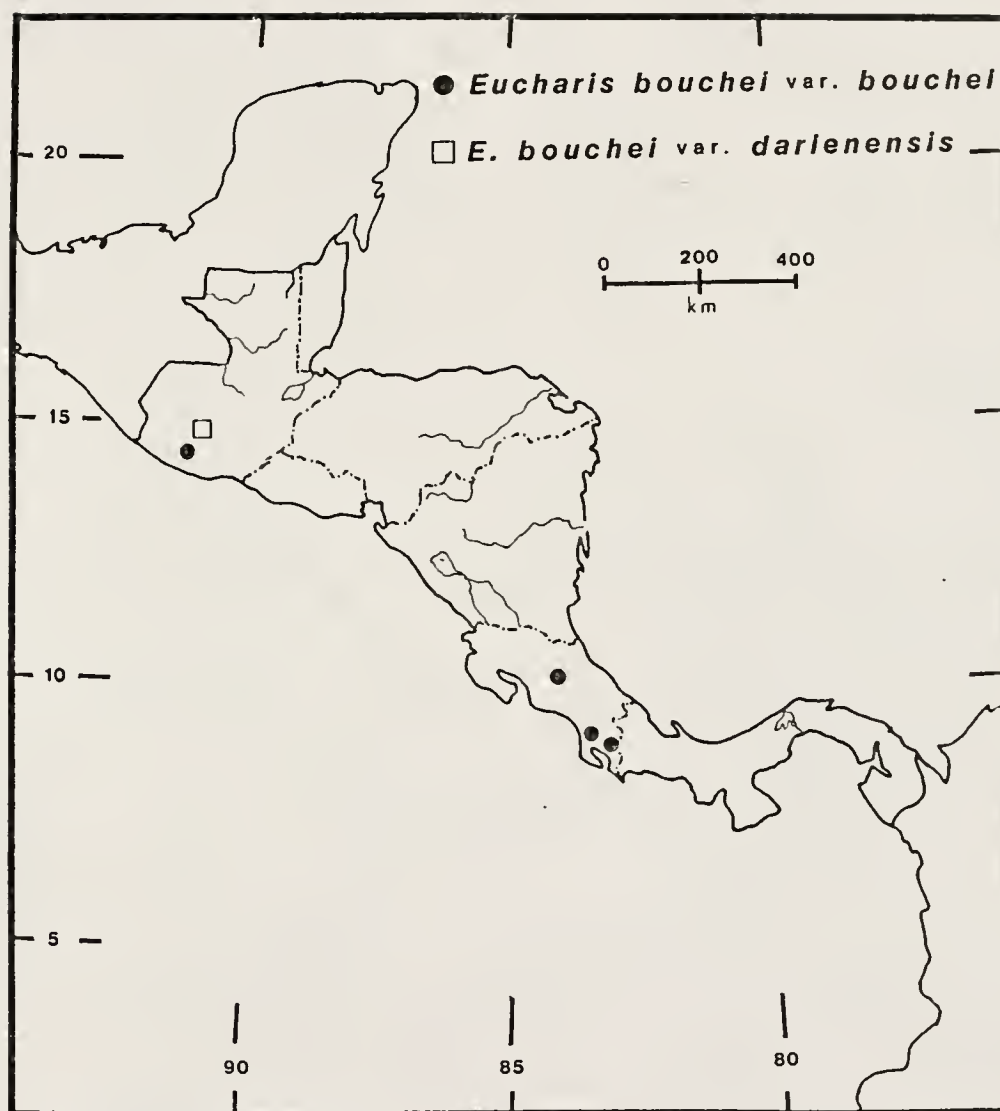


Figure 12.14. Eucharis astrophiala, adapted from a drawing by  
Boots N. Culberston of Dodson et al. 7122, SEL. A. Habit.  
B. Inflorescence. C. Flower, longitudinal section. D.  
Stigma. E. Ovary, longitudinal section.

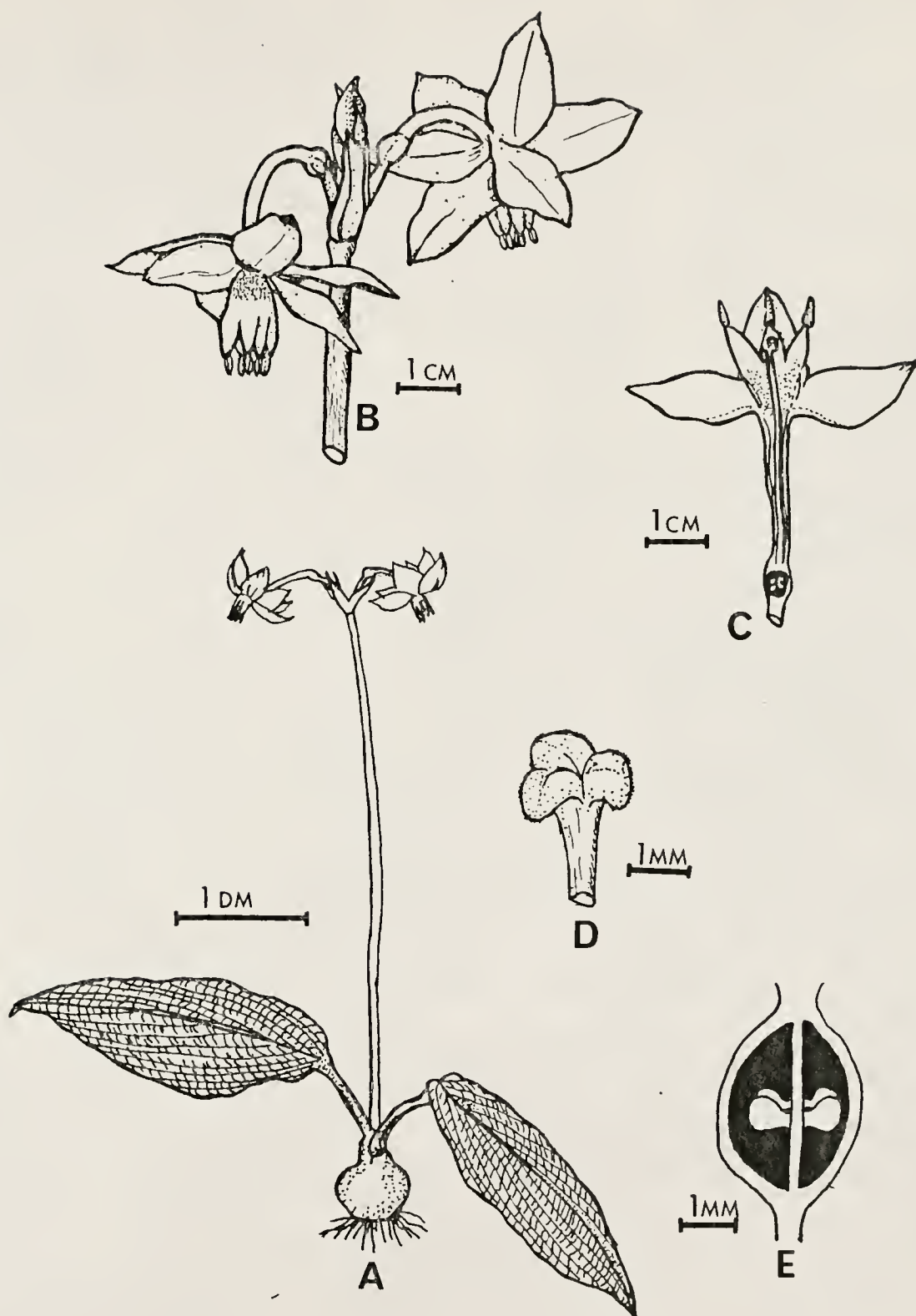




Figure 12.15. Distribution of Eucharis astrophiala in Ecuador.



Figure 12.16. *Eucharis cyaneosperma* and *E. ulei*. A. Flower of *E. cyaneosperma* (holotype, Meerow 1032, FLAS). B. Flower of *E. ulei* (Schunke 1887, F). C. Ovary of *E. ulei*, longitudinal section (Schunke 1887, F).

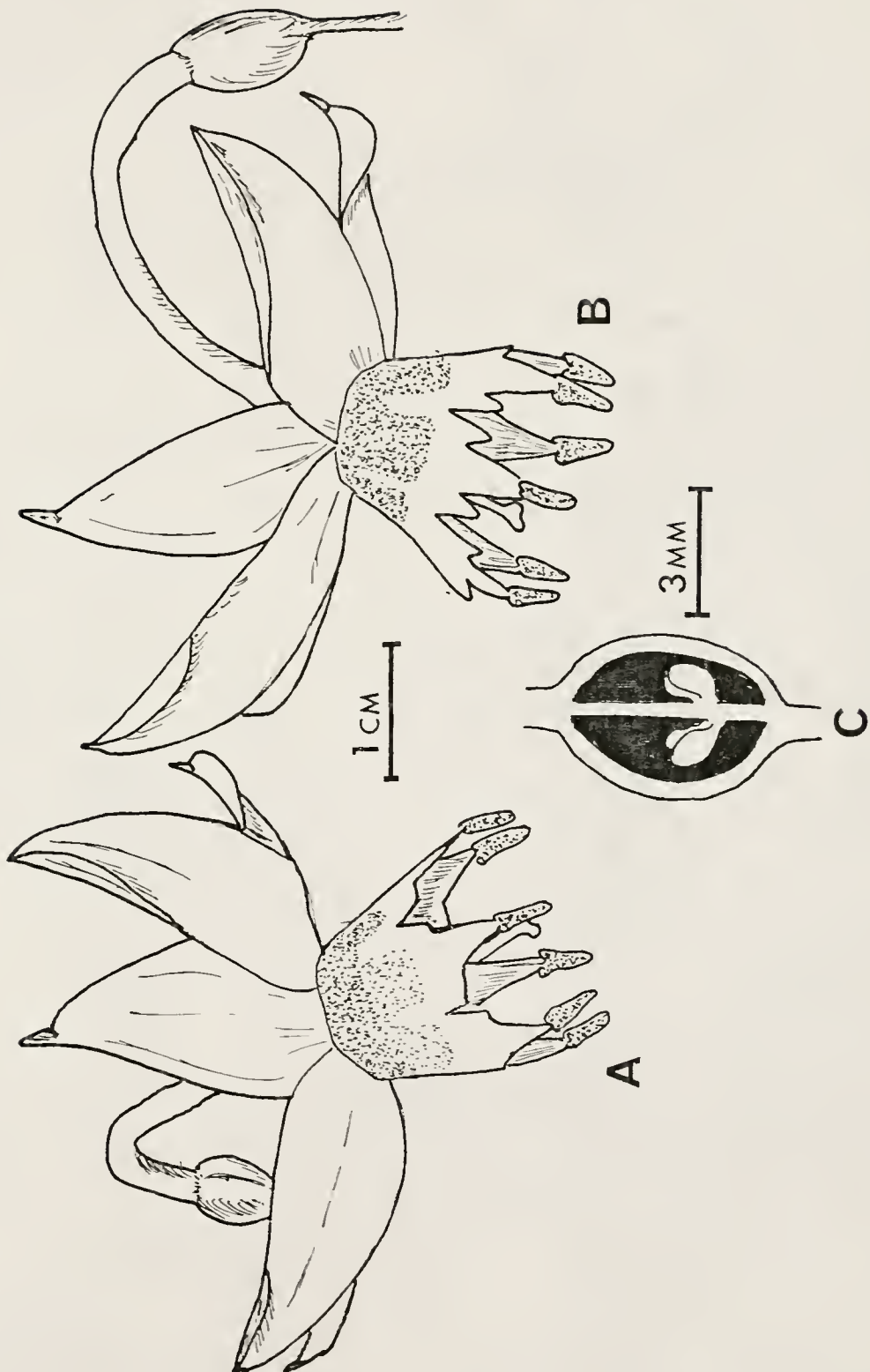


Figure 12.17. Eucharis corynandra, E. lehmannii and E. oxyandra.  
A-C. E. oxyandra (isotype: Hutchison et al. 5983, UC). A. Flower. B. Androecium. Note the polymorphism. C. Ovary, longitudinal section. D-F. E. lehmannii [after tab. 1300 in Regel (1889), and a photo of the type (LE)]. D. Flower. E. Staminal cup. F. Ovary, longitudinal section. G-I. E. corynandra (isotype, Ravenna 2090, K). G. Flower. H. Staminal cup. I. Ovary, longitudinal section.

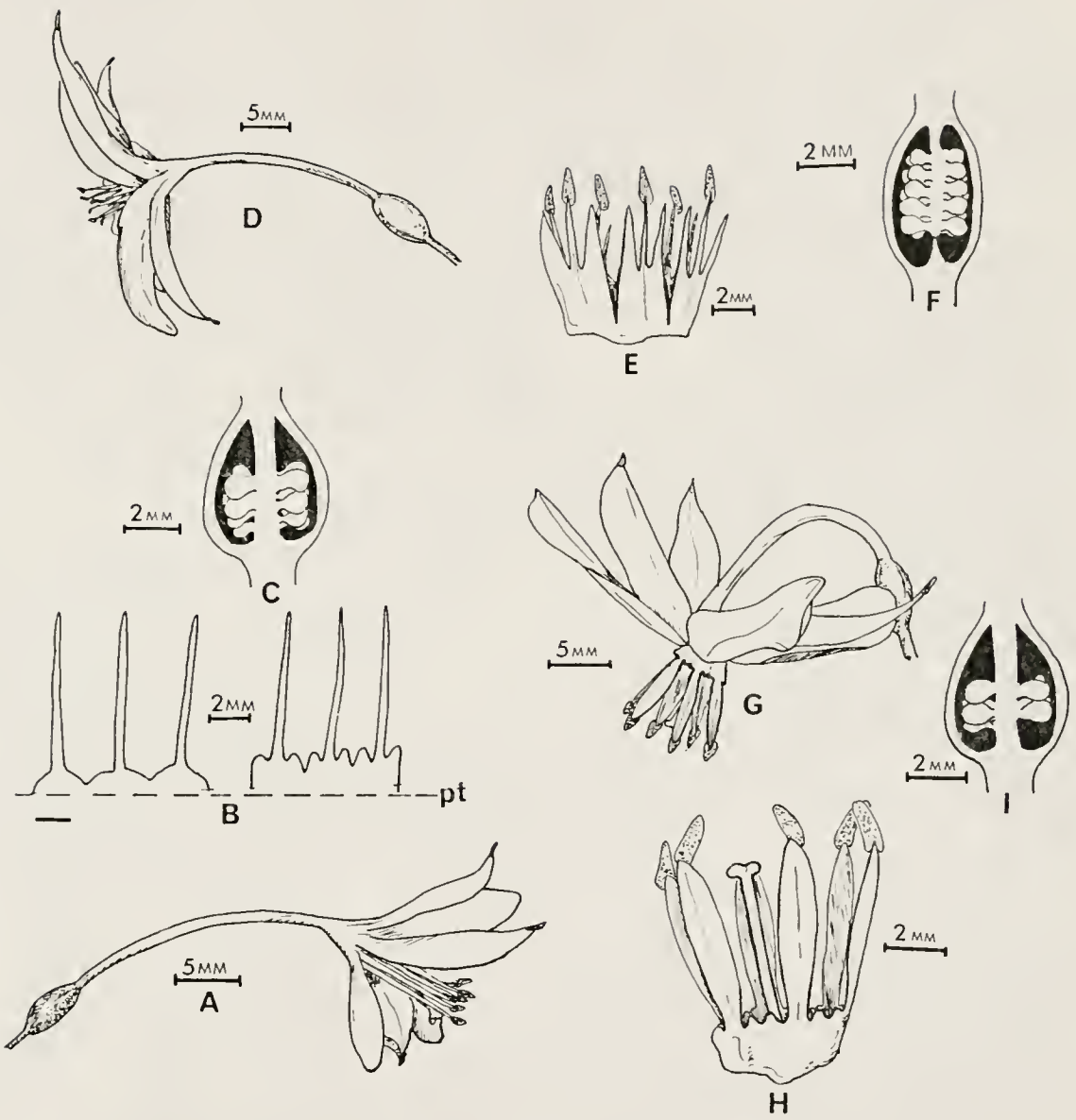




Figure 12.18. Distributions of Eucharis castelnaeana, E. corynandra, E. lehmanni, E. oxyandra, and E. plicata in northwestern-central South America.

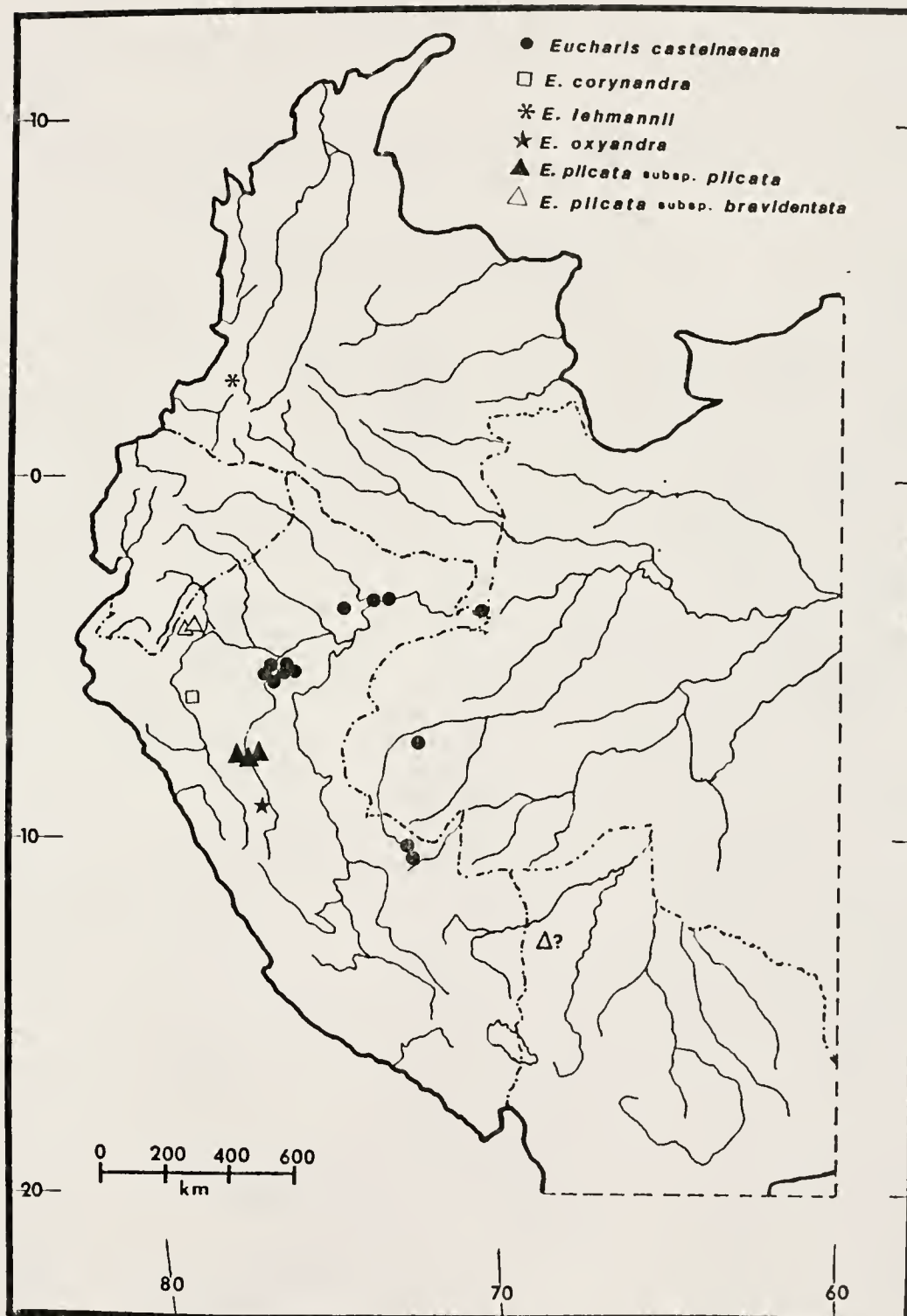


Figure 12.19. Eucharis plicata (Meerow et al. 1025, FLAS). A. Habit. B. Inner tepal. C. Outer tepal. D. Stigma. E. Staminal cup. F. Ovary, longitudinal section. G. Ovary, transverse section.

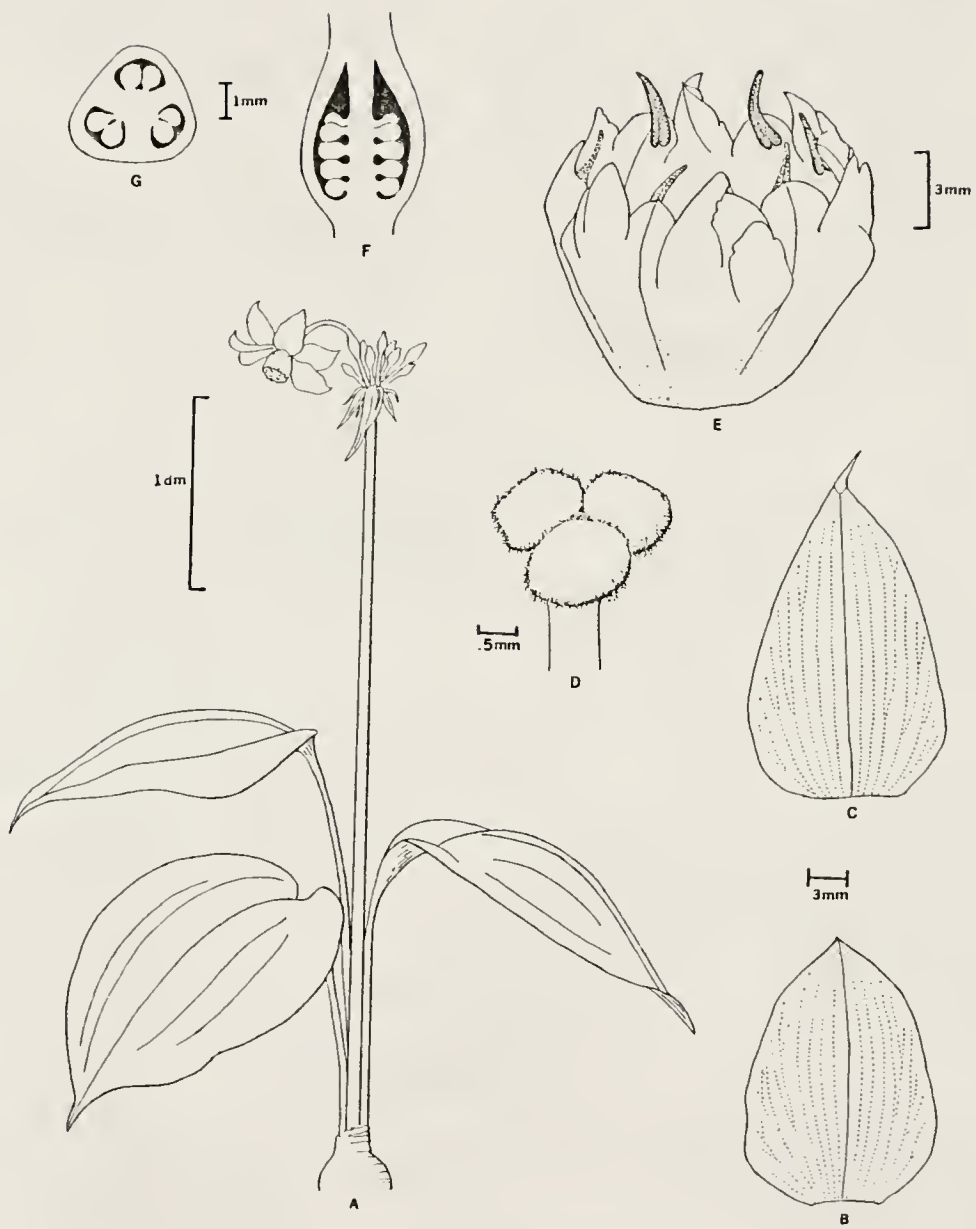


Figure 12.20. *Eucharis castelnaeana*. A. Flowers. i. Schunke  
14154-A, FLAS. ii. Schunke 14156. Note varying habit of  
limb. B. Tepals (Schunke 14156). i. Outer tepal. ii.  
Inner tepal. C. Staminal cup (Schunke 14156). D. Ovary  
(Schunke 14156), longitudinal section.

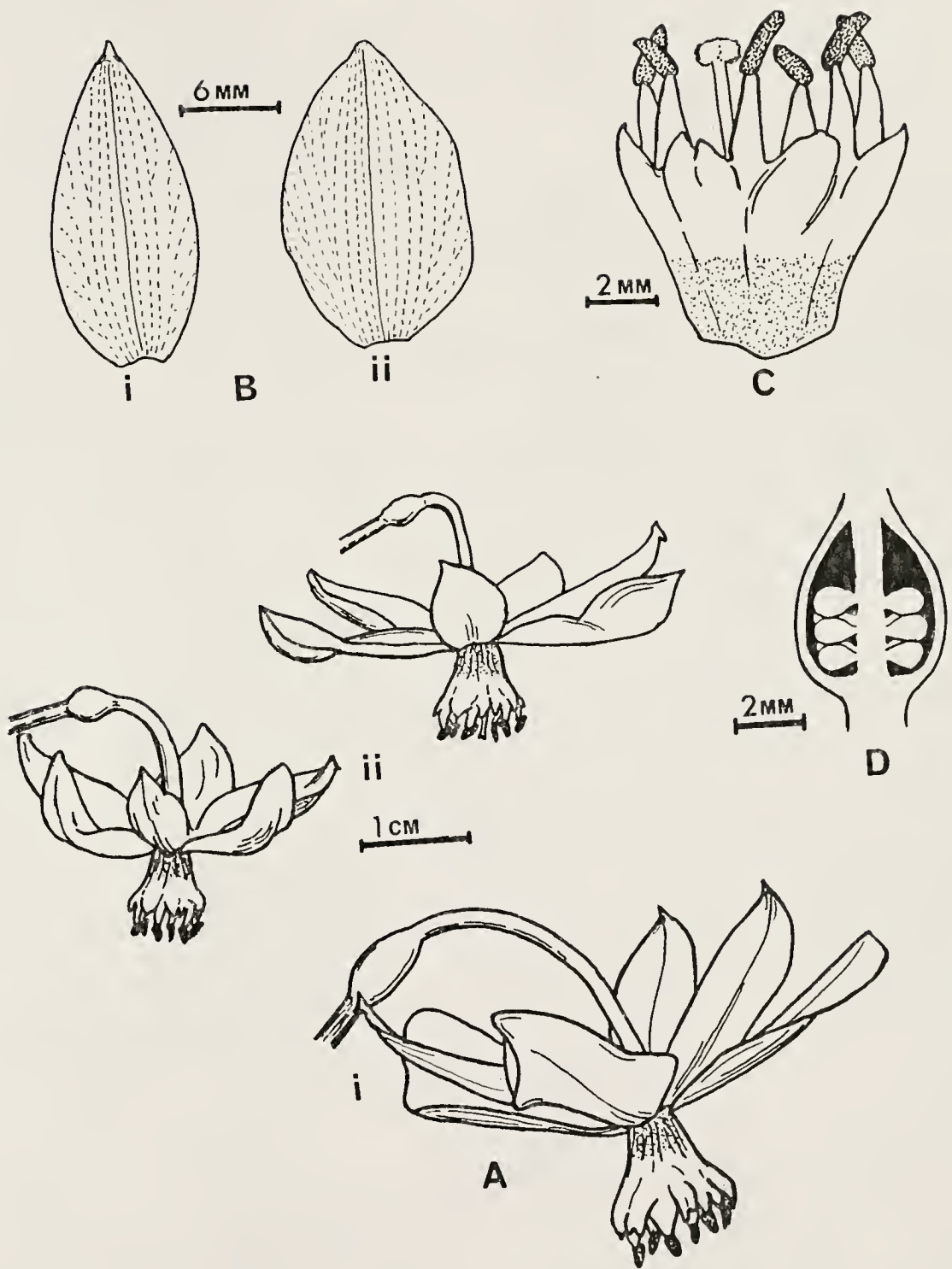




Figure 12.21. Natural hybrids of Eucharis subg. Heterocharis. A-C. E. X grandiflora. A. Flower of "mastersii" form (Madison et al. s. n., SEL). B-C. "Lowii" form (Meerow & Teets 1127, FLAS). B. Habit in Colombia. C. Flower. D-E. X Calicharis butcheri (Meerow 1098, FLAS). D. Inflorescences. E. Flower.

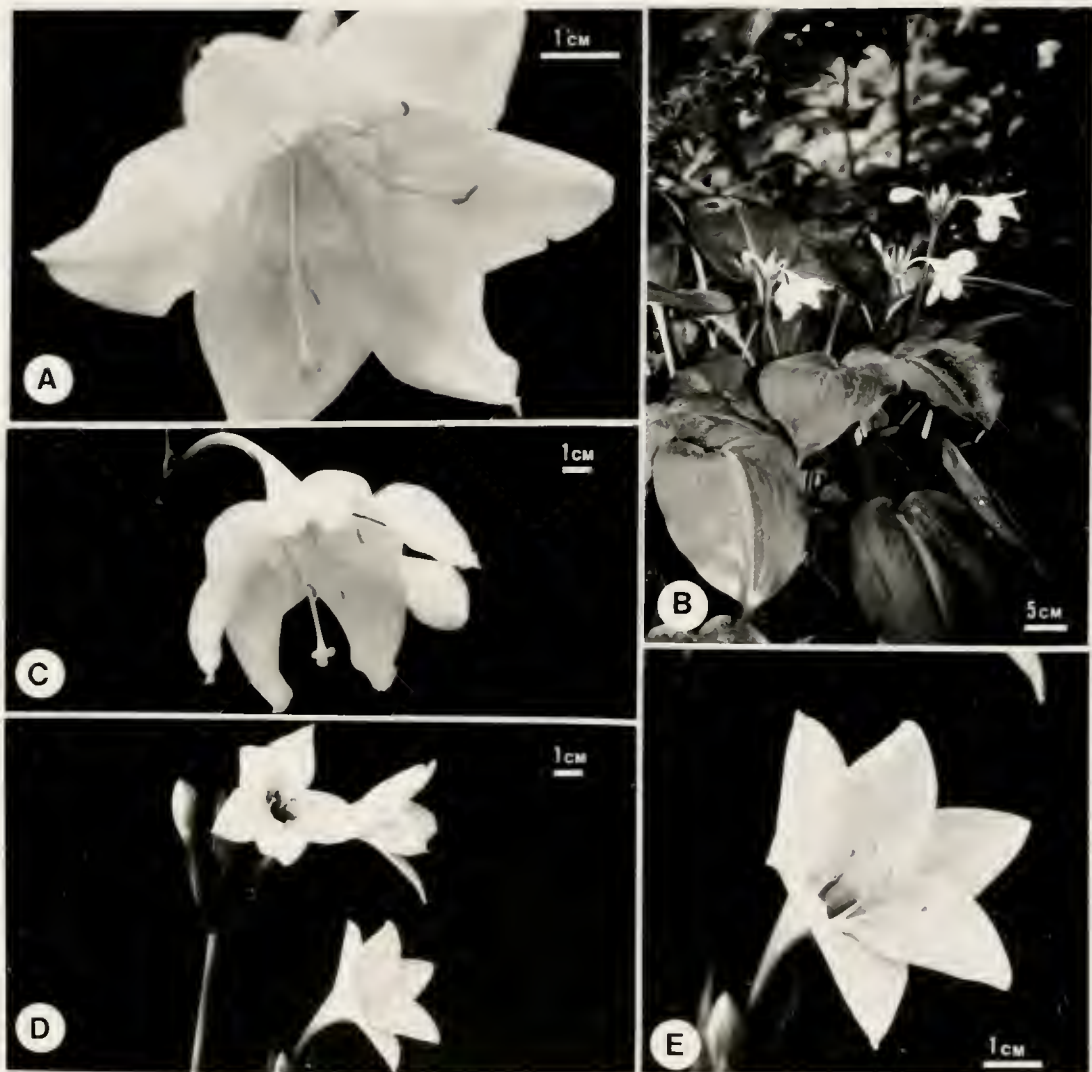


Figure 12.22. Distributions of species and hybrids of Eucharis  
subg. Heterocharis in northwestern-central South America.



Figure 12.23. Eucharis sanderi (Cuatrecasas 16380, F). A. Habit.  
B. Flower. C. Tepals. i. Outer tepal. ii. Inner tepal.  
D. Detail of androecium. E. Ovary, longitudinal section.

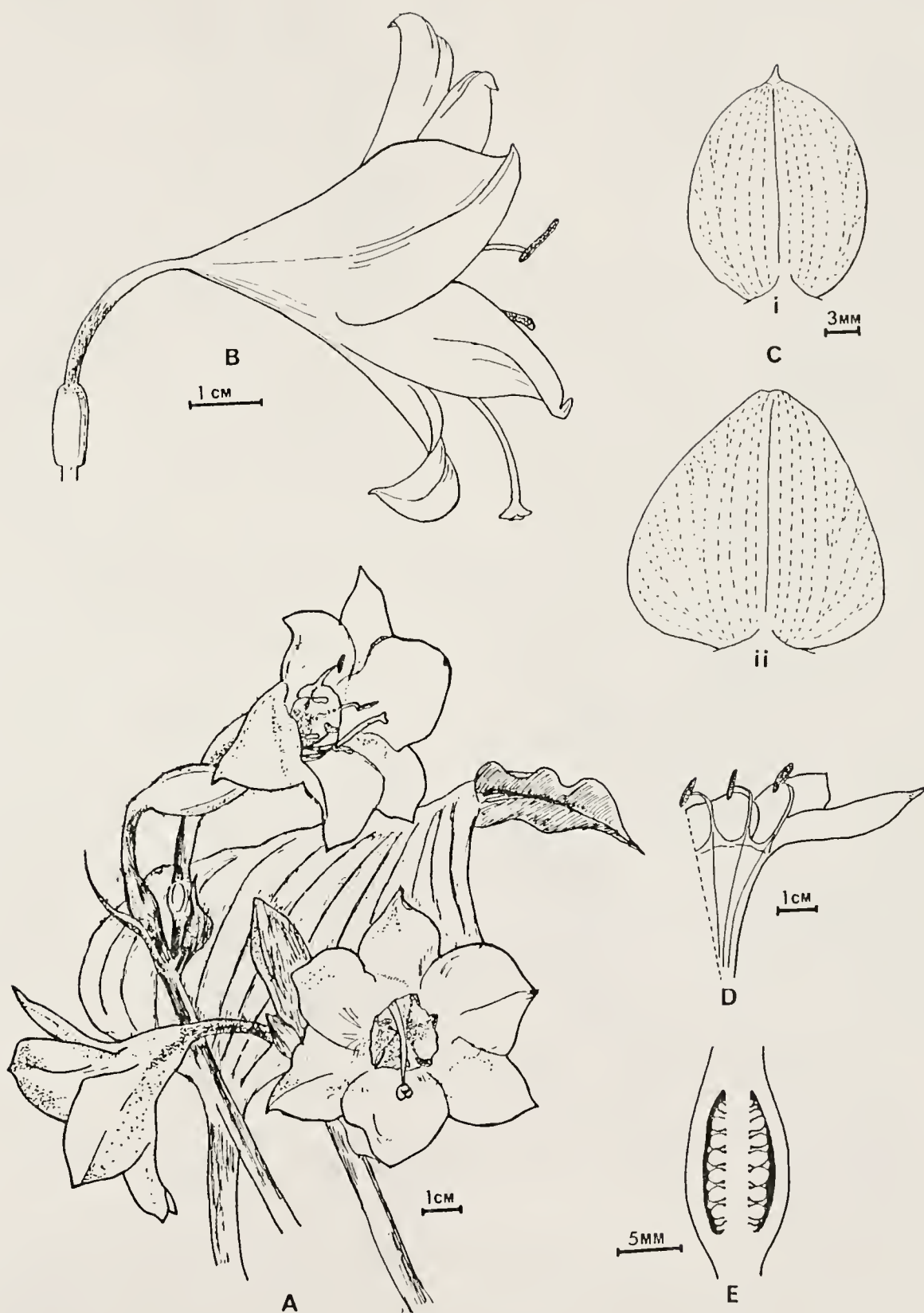




Figure 12.24. Eucharis anomala, after a drawing by Wendy B.  
Zomleffer of Dodson 5527 (SEL). A. Habit. B. Flower. C.  
Ovary, longitudinal section.

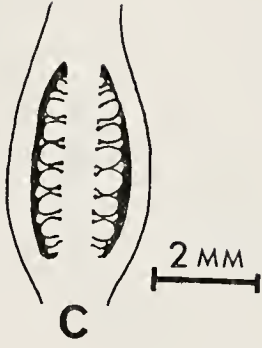
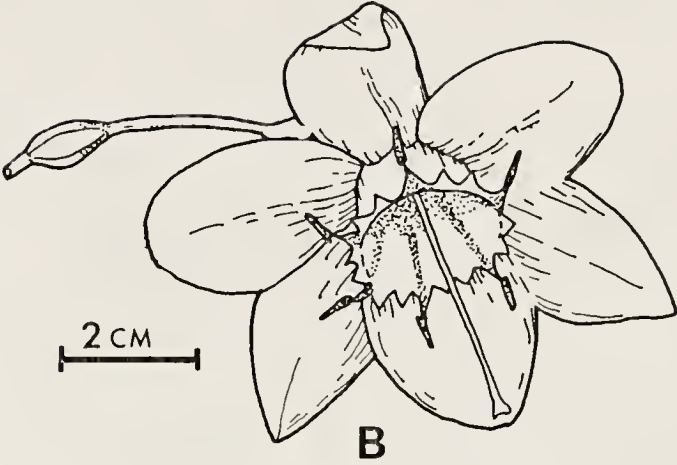
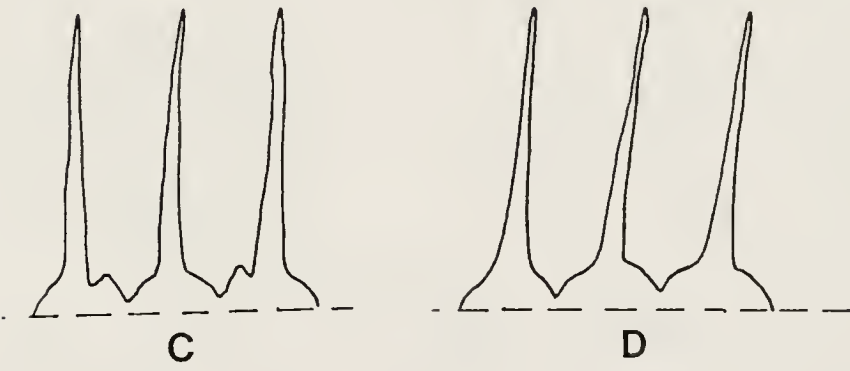
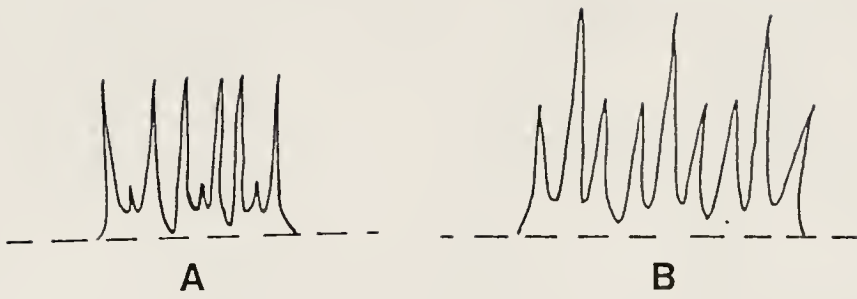


Figure 12.25. Eucharis anomala and E. amazonica. A-B. E. anomala (Meerow 1141, FLAS). C-D. E. amazonica (Schunke 14179, FLAS).



Figure 12.26. Androecial morphology of Caliphruria. A. C. tenera  
(Triana 1289, COL). B. C. hartwegiana (neotype, Lehmann  
6376, K). C-D. C. subedentata. C. Pittier 1009, US. D.  
Holotype, ex hort. Beaufoy s. n., K. E. C. korsakoffii  
(Meerow 1096, F).



5 mm





Figure 12.27. Distribution of species of Caliphurria in  
northwestern-central South America.



Figure 12.28. *Caliphruria subdentata* (Meerow 1123, FLAS). A. Habit. B. Flower. C. Tepals. i. Outer tepal. ii. Inner tepal. D. Longitudinal section through part of flower to show detail of androecium. E. Ovary, longitudinal section.

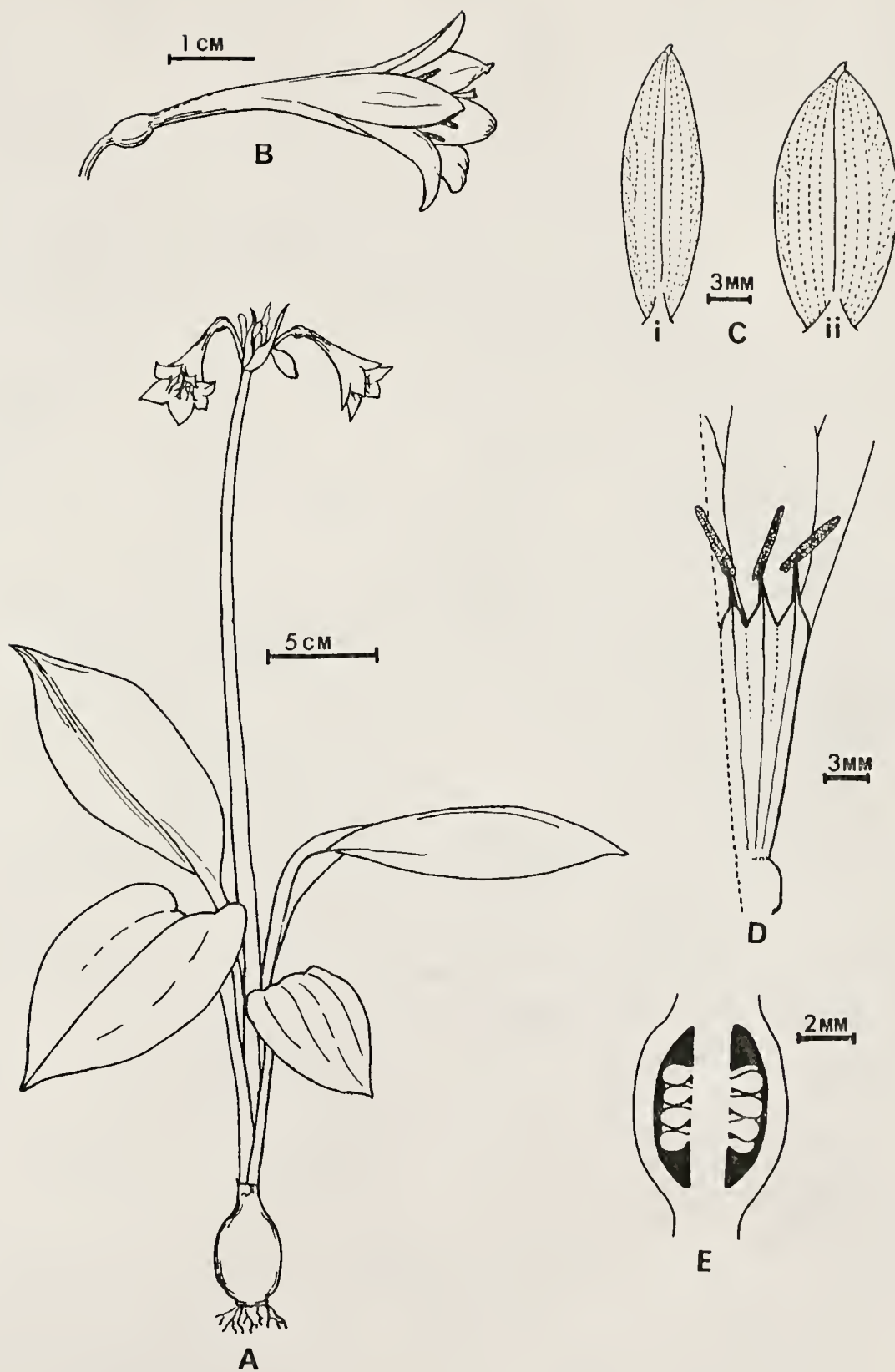


Figure 12.29. Caliphruria korsakoffii (Meerow 1096). A.  
Inflorescence. B. Flower.





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# APPENDIX

Table A.1. Operational taxonomic units (OTU's) for multivariate analysis of Amazonian Eucharis.

NO.	COLLECTION AND HERBARIUM	SPECIES	ORIGIN
1	Harling et al. 7201 (GB)	formosa	Ecuador
2	Harling & Andersson 17374 (GB)	formosa	Ecuador
3	Dodson 6636 (SEL)	formosa	Ecuador
4	Holguer 2655 (GB)	formosa	Ecuador
5	Asplund 9488 (S)	formosa	Ecuador
6	Harling 7400 (GB)	candida	Ecuador
7	Besse et al. 1598 (SEL)	candida	Ecuador
8	Besse et al. 1643 (SEL)	candida	Ecuador
9	Asplund 8853 (S)	candida	Ecuador
10	Besse et al. 1558 (SEL)	candida	Ecuador
		X formosa	
11	Besse et al. 1563 (SEL)	candida	Ecuador
		X formosa	
12	Holguer 3532 (GB)	formosa	Ecuador
13	Holguer 2960 (GB)	formosa	Ecuador
14	Prescott 438 (NY)	formosa	Ecuador

Table A.1--continued.

NO.	COLLECTION AND HERBARIUM	SPECIES	ORIGIN
15	Asplund 19571 (S)	formosa	Ecuador
16	Benoist 4717 (P)	candida	Ecuador
17	Meerow 1103 (FLAS)	formosa	Ecuador
18	Schunke 14154A (FLAS)	castelnaeana	Peru
19	Schunke 14156 (FLAS)	castelnaeana	Peru
20	Ferreyra 4984 (MO)	castelnaeana	Peru
21	Huber 1514 (GOEL)	castelnaeana	Peru
22	Berlin 148 (NY)	plicata subsp. brevidentata	Peru
23	Killip & Smith 27844 (US)	castelnaeana	Peru
24	Williams 1896 (F)	castelnaeana	Peru
25	Castelnau s. n. (P)	castelnaeana	Peru
26	Killip & Smith 28886 (US)	castelnaeana	Peru
27	Killip & Smith 28249 (US)	castelnaeana	Peru
28	Meerow et al. 1025 (FLAS)	plicata subsp. plicata	Peru
29	Plowman et al. 11394 (FLAS)	plicata subsp. plicata	Peru
30	Meerow 1143 (FLAS)	plicata subsp. brevidentata	Bolivia
31	Ule 5737A (B)	ulei	Brazil
32	Ferreira s.n. (P)	ulei	Brazil
33	Sandeman 3724 (K)	cyaneosperma	Peru

Table A.1--continued.

NO.	COLLECTION AND HERBARIUM	SPECIES	ORIGIN
34	Tessman 3179 (NY)	cyaneosperma	Peru
35	Diaz-M 15 (COL)	ulei	Colombia
36	White 930 (NY)	ulei	Bolivia
37	Killip & Smith 27442 (US)	ulei	Peru
38	Schunke 1887 (F)	ulei	Peru
39	Harling & Andersson 12915 (GB)	formosa	Ecuador
40	Harling et al. 7673 (GB)	formosa	Ecuador
41	Holguer 1504 (GB)	formosa	Ecuador
42	Hitchcock 21891 (US)	formosa	Ecuador
43	Penland & Summers 142 (US)	formosa	Ecuador
44	Gutierrez 2687 (COL)	candida	Ecuador
45	Mexia 6855 (US)	formosa	Ecuador
46	Asplund 9122 (S)	formosa	Ecuador
47	Asplund 19120 (S)	formosa	Ecuador
48	Harling & Andersson 11682 (GB)	candida	Ecuador
49	Harling & Andersson 11719A (GB)	formosa	Ecuador
50	Plowman & Kennedy 5811 (GH)	ulei	Peru
51	Idrobo & Schultes 1208 (US)	candida	Colombia
52	Plowman et al. 6724 (F)	candida	Peru
53	Schunke 3856 (F)	formosa	Peru
54	Von Sneidern s. n. (S)	formosa	Colombia
55	Lozano 594 (COL)	formosa	Colombia
56	Revilla 990 (MO)	formosa	Peru

Table A.1--continued.

NO.	COLLECTION AND HERBARIUM	SPECIES	ORIGIN
57	De Jussieu s. n.	ulei	Peru
58	Huashikat 164 (MO)	candida	Peru
59	Ducke 12162 (GOEL)	cyaneosperma	Brazil
60	Krukoff 5573 (NY)	cyaneosperma	Brazil
61	Nelson 88-301 (MO)	cyaneosperma	Bolivia
62	Killip s. n. (COL)	formosa	Colombia
63	Goudot s. n. (P)	bonplandii	Colombia
64	Pennell et al. 8604 (US)	bonplandii	Colombia
65	Uribe 4218 (COL)	bonplandii	Colombia
66	Schunke 9675 (F)	formosa	Peru
67	Killip & Smith 27656 (US)	ulei	Peru
68	Seibert 2145 (US)	cyaneosperma	Peru
69	Killip et al. 29227 (US)	ulei	Peru
70	Schunke 14157 (FLAS)	formosa	Peru
71	Schunke 14155B (FLAS)	candida	Peru
72	Schunke 14174 (FLAS)	formosa	Peru
73	Cabrera 3336 (COL)	formosa	Colombia
74	Schultes & Black 8478 (US)	candida	Colombia
75	Krukoff 4613 (NY)	ulei	Brazil
76	Ancuash 161 (MO)	formosa	Peru
77	Cardenas 1553A (NY)	cyaneosperma	Bolivia
78	Meerow 1108 (FLAS)	bakeriana	Peru

Table A.2. Data matrix for multivariate analyses of Amazonian Eucharis.

		CHARACTER																
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
OTU																		
1	1	10	75	5.7	2.7	6.0	33.0	10.0	44.0	39.0	19.0	25.0	10.0	16.2	1	1	1	5
2	2	10	58	6.2	2.2	5.0	34.0	10.0	30.5	29.0	14.0	18.0	11.6	16.8	1	1	1	4
3	3	06	65	5.8	2.5	5.6	35.0	10.0	40.8	36.0	13.0	16.0	16.0	19.0	1	2	1	5
4	4	10	75	6.5	2.5	6.5	37.0	14.2	37.5	35.2	17.0	22.6	12.5	21.0	2	1	1	5
5	5	10	75	4.9	2.2	6.3	40.0	10.0	42.0	40.0	15.5	21.0	13.5	23.0	1	2	1	5
6	6	05	43	3.5	1.5	4.7	26.0	12.5	27.5	23.5	10.5	13.5	16.8	09.0	2	1	1	2
7	7	07	50	3.7	1.2	3.5	30.0	07.5	26.5	26.0	11.0	13.0	11.3	10.0	3	2	1	6
8	8	10	40	4.0	1.2	3.5	28.0	09.2	26.0	23.0	14.0	17.0	10.0	15.0	3	2	1	4
9	9	10	46	3.5	1.3	5.4	28.5	07.3	20.7	20.5	14.4	13.4	10.0	14.5	1	2	2	5
10	10	08	55	4.5	2.0	5.2	35.0	09.2	31.0	28.0	12.0	18.0	10.0	15.5	1	2	1	3
11	11	08	55	4.0	1.5	4.0	31.0	07.8	32.0	30.0	13.0	17.0	10.0	15.0	1	3	1	6
12	12	08	55	4.7	2.7	6.7	36.6	14.2	29.0	27.0	14.0	19.0	09.0	17.5	1	2	1	5



Table A.2--continued.

		CHARACTER																
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
OTU																		
113	10	60	6.0	2.5	7.5	34.0	09.4	27.6	25.0	13.5	16.5	08.5	21.0	2	2	1	5	
114	10	70	4.2	1.7	4.8	30.0	12.0	43.3	40.0	12.0	15.5	17.2	19.3	2	3	1	5	
115	06	74	4.0	2.5	7.0	35.0	10.0	35.0	32.5	18.0	21.0	12.8	22.5	2	1	1	4	
116	08	40	6.4	1.0	2.6	30.0	04.6	07.5	11.5	25.0	23.0	07.6	09.4	1	2	1	4	
117	10	72	5.2	2.0	6.2	34.0	11.5	40.0	37.5	18.0	21.5	10.5	14.2	1	3	1	5	
118	08	47	2.8	1.8	3.8	21.5	04.0	23.0	21.0	07.0	11.0	08.0	10.0	2	1	2	3	
119	10	35	1.8	1.5	4.0	17.0	04.8	17.5	14.5	09.0	11.0	06.0	09.3	2	1	2	4	
120	06	27	1.7	0.9	2.0	12.5	04.6	15.5	15.4	04.3	06.2	05.8	06.4	2	1	1	3	
121	09	35	4.0	1.5	5.0	27.0	05.5	20.0	20.0	05.0	09.0	08.0	12.0	2	1	1	3	
122	04	40	1.2	1.0	3.7	25.5	07.5	20.0	20.0	09.0	12.0	08.5	10.2	2	2	2	4	
123	10	31	2.5	1.2	3.0	22.0	05.5	16.0	15.0	06.5	08.5	05.0	09.0	2	1	1	5	
124	06	42	2.5	1.5	3.8	20.0	05.8	20.0	18.5	10.0	13.0	07.0	10.6	2	1	2	5	

Table A.2--continued.

CHARACTER																
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
OTU																
25	05	25	1.5	1.0	2.7	15.0	03.0	14.0	11.5	04.0	06.0	05.5	07.0	2	1	1
26	10	32	2.2	1.6	4.0	19.5	07.5	16.0	14.2	06.0	08.0	05.0	12.0	2	2	5
27	10	30	2.0	1.8	4.0	17.5	06.5	18.0	17.0	07.0	09.5	07.0	11.5	2	2	7
28	10	30	3.0	1.9	3.5	22.0	06.0	18.0	16.0	10.0	12.0	10.5	12.0	2	2	8
29	10	38	5.0	2.0	4.5	22.0	05.5	23.0	23.0	09.0	11.0	12.7	14.7	2	2	8
30	10	36	3.5	1.5	6.0	30.0	08.8	20.0	18.7	12.0	15.0	08.0	11.0	2	1	6
31	05	42	2.8	1.0	4.3	29.0	06.5	28.0	26.0	08.0	09.0	10.0	12.5	2	1	2
32	05	50	4.3	1.8	5.0	26.0	06.0	32.0	29.5	10.5	13.5	14.0	14.3	2	2	2
33	03	40	2.7	1.5	3.5	25.0	07.5	28.0	23.5	08.5	10.9	10.7	12.8	3	3	2
34	03	55	5.7	1.5	5.4	35.0	08.0	35.0	32.0	14.0	19.6	11.5	16.5	3	1	4
35	06	50	5.5	1.7	4.5	31.7	11.0	25.6	24.6	11.0	16.6	14.3	15.5	1	2	2
36	07	42	5.8	1.8	3.7	33.0	10.0	27.0	25.0	10.0	13.5	10.0	12.5	1	1	2

Table A.2--continued.

		CHARACTER															
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
OTU																	
37	05	52	6.0	1.8	4.0	37.4	10.0	24.0	23.0	17.3	13.0	10.8	14.0	1	1	1	2
38	05	53	6.0	1.5	4.0	30.0	07.0	26.3	24.5	08.3	11.5	10.6	11.0	1	1	1	2
39	10	65	6.2	2.0	6.2	45.0	10.8	40.0	39.0	17.0	20.0	13.0	22.0	4	2	0	5
40	08	70	6.0	2.5	6.0	36.0	12.0	40.0	36.0	13.5	17.5	09.5	14.0	5	2	0	6
41	10	60	7.4	2.2	4.5	42.0	11.0	28.5	25.2	10.6	13.2	08.2	16.0	5	2	0	2
42	10	70	6.0	3.0	6.5	35.0	12.0	45.0	43.0	17.0	20.0	10.0	18.5	3	3	1	6
43	05	70	4.0	2.0	6.0	42.0	11.0	45.6	38.7	15.4	20.5	13.8	20.0	5	3	0	4
44	05	45	4.6	2.0	4.3	22.0	07.2	26.0	23.0	07.0	12.0	07.0	13.5	5	3	0	4
45	06	60	5.1	2.5	7.3	39.0	10.0	33.8	30.0	10.0	17.0	09.0	20.0	5	3	0	6
46	10	80	5.2	2.5	5.8	39.0	12.0	38.0	36.0	15.6	19.0	10.2	22.5	5	2	0	8
47	04	59	5.6	2.6	7.0	33.0	10.5	30.0	29.0	13.0	15.0	11.6	18.6	5	2	0	5
48	06	40	3.5	1.7	3.8	30.8	11.8	23.0	22.0	09.0	14.0	11.0	17.2	3	2	1	2

Table A.2--continued.

		CHARACTER															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
OTU																	
49	10	58	6.0	2.0	6.0	44.5	11.0	26.0	25.0	12.0	16.2	13.8	18.2	5	2	0	6
50	05	53	4.5	1.5	5.2	31.0	10.0	29.0	26.8	08.5	12.0	12.0	17.0	5	2	0	2
51	08	45	4.7	1.9	4.3	30.0	10.5	26.6	23.6	10.5	12.0	11.2	14.0	3	3	1	3
52	06	60	5.3	1.8	4.5	28.0	12.3	31.0	28.0	11.0	15.0	10.0	20.0	5	3	0	3
53	05	73	4.0	2.0	7.1	36.8	13.0	30.8	31.5	15.7	23.5	12.2	20.0	5	3	0	5
54	10	55	5.5	2.0	4.0	38.8	11.0	35.2	33.0	10.5	16.5	10.0	15.2	5	2	0	4
55	07	60	5.9	2.8	4.5	27.5	08.5	33.5	32.5	15.5	20.5	08.0	17.0	5	3	0	4
56	05	55	5.4	2.5	5.6	34.0	12.0	32.0	30.0	14.5	19.2	10.6	18.5	5	2	0	5
57	05	50	5.0	1.7	4.4	35.0	08.2	30.5	28.0	11.0	15.0	12.4	15.5	5	2	0	3
58	04	55	5.5	2.2	5.0	34.5	10.2	26.2	24.5	14.4	19.5	09.5	16.0	5	2	0	3
59	05	36	4.5	1.6	3.7	35.0	07.5	23.5	21.5	10.0	13.2	09.5	13.3	4	2	1	2
60	04	40	6.0	1.5	3.5	35.5	06.0	26.0	24.0	04.8	06.5	07.5	08.0	4	2	1	2

Table A.2--continued.

		CHARACTER																
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
OTU																		
61	05	40	3.7	1.5	3.5	34.5	09.0	25.0	23.0	11.0	13.8	11.0	13.0	4	1	1	2	
62	06	74	4.3	1.5	5.9	55.7	05.0	47.7	41.0	11.0	16.4	17.0	18.2	3	1	1	4	
63	04	25	3.5	1.4	3.5	24.5	08.8	25.0	24.0	06.4	07.5	09.0	11.5	1	2	1	3	
64	07	57	5.8	2.0	4.4	33.7	10.3	30.5	26.0	09.5	14.8	14.3	13.0	1	2	1	2	
65	07	50	5.5	1.5	3.6	31.5	08.0	29.7	28.2	08.1	11.5	10.0	11.7	1	2	1	2	
66	10	60	4.7	1.8	5.5	36.0	09.0	35.5	32.5	14.4	18.8	14.0	20.0	2	1	1	9	
67	05	50	6.9	1.8	4.9	38.0	10.7	27.8	26.0	08.0	12.0	09.5	16.5	2	1	1	3	
68	05	56	6.1	1.5	4.5	56.7	06.0	30.2	29.7	12.7	16.8	10.6	11.7	2	1	1	3	
69	07	45	5.5	1.5	4.5	37.5	09.5	29.5	25.8	09.5	14.6	10.5	16.0	2	1	1	3	
70	09	65	4.0	2.0	5.0	40.0	13.0	31.5	30.0	14.0	16.0	11.0	13.0	5	3	0	6	
71	05	50	4.5	1.8	5.0	26.5	10.0	24.5	22.0	11.0	14.5	08.5	13.0	5	3	0	4	
72	10	42	6.5	1.8	5.7	41.7	08.3	39.7	36.0	13.0	16.0	18.0	18.0	1	3	1	5	

Table A.2--continued.

		CHARACTER																
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
OTU																		
73	10	65	5.0	2.1	6.0	35.5	12.5	29.5	27.0	12.0	18.0	16.2	16.2	16.2	1	3	1	2
74	10	60	5.7	1.5	6.0	30.0	10.0	30.0	29.0	14.5	19.5	20.0	20.0	20.0	5	3	0	2
75	05	40	3.5	1.5	4.0	25.0	08.3	24.0	21.0	06.5	10.0	13.0	13.0	13.0	1	3	1	3
76	06	65	4.3	2.5	5.0	41.5	08.3	20.8	23.0	31.3	32.2	18.2	18.2	18.2	2	3	1	4
77	07	45	5.0	2.0	5.0	32.0	08.5	25.0	23.0	13.0	15.0	17.0	17.0	17.0	4	3	1	2
78	10	60	3.0	1.7	6.4	35.0	09.7	32.0	32.0	16.8	21.0	16.0	13.0	13.0	1	1	2	8



Table A.3. Operational taxonomic units (OTU's) for multivariate analysis of androecial characters of Amazonian Eucharis.

NO.	COLLECTION AND HERBARIUM	SPECIES	ORIGIN
1	Harling et al. 7201 (GB)	formosa	Ecuador
2	Harling & Andersson 17374 (GB)	formosa	Ecuador
3	Dodson 6636 (SEL)	formosa	Ecuador
4	Holguer 2655 (GB)	formosa	Ecuador
5	Asplund 9488 (S)	formosa	Ecuador
6	Harling 7400 (GB)	candida	Ecuador
7	Besse et al. 1598 (SEL)	candida	Ecuador
8	Besse et al. 1643 (SEL)	candida	Ecuador
9	Asplund 8853 (S)	candida	Ecuador
10	Besse et al. 1558 (SEL)	candida	Ecuador
		X formosa	
11	Besse et al. 1563 (SEL)	candida	Ecuador
		X formosa	
12	Holguer 3532 (GB)	formosa	Ecuador
13	Holguer 2960 (GB)	formosa	Ecuador
14	Prescott 438 (NY)	formosa	Ecuador
15	Asplund 19571 (S)	formosa	Ecuador
16	Benoist 4717 (P)	candida	Ecuador
17	Meerow 1103 (FLAS)	formosa	Ecuador
18	Schunke 14154A (FLAS)	castelnaeana	Peru
19	Schunke 14156 (FLAS)	castelnaeana	Peru
20	Ferreyra 4984 (MO)	castelnaeana	Peru
21	Huber 1514 (GOEL)	castelnaeana	Peru

Table A.3--continued.

NO.	COLLECTION AND HERBARIUM	SPECIES	ORIGIN
22	Berlin 148 (NY)	plicata subsp. brevidentata	Peru
23	Killip & Smith 27844 (US)	castelnaeana	Peru
24	Williams 1395 (F)	castelnaeana	Peru
25	Castelnau s. n. (P)	castelnaeana	Peru
26	Killip & Smith 28886 (US)	castelnaeana	Peru
27	Killip & Smith 28249 (US)	castelnaeana	Peru
28	Meerow et al. 1025 (FLAS)	plicata subsp. plicata	Peru
29	Plowman et al. 11394 (FLAS)	plicata subsp. plicata	Peru
30	Ule 5737A (B)	ulei	Brazil
31	Ferreira s.n. (P)	ulei	Brazil
32	Sandeman 3724 (K)	cyaneosperma	Peru
33	Tessman 3179 (NY)	cyaneosperma	Peru
34	Schunke 3396 (F)	ulei	Peru
35	Diaz-M 15 (COL)	ulei	Colombia
36	White 930 (NY)	ulei	Bolivia
37	Mexia 6504A (US)	ulei	Peru
38	Williams 2629 (F)	ulei	Peru
39	Killip & Smith 27442 (US)	ulei	Peru
40	Schunke 1887 (F)	ulei	Peru
41	Croat 19289 (MO)	ulei	Peru

Table A.3--continued.

NO.	COLLECTION AND HERBARIUM	SPECIES	ORIGIN
42	Krukoff 4613 (NY)	ulei	Brazil
44	Harling & Andersson 12915 (GB)	formosa	Ecuador
45	Harling et al. 7673 (GB)	formosa	Ecuador
46	Holguer 1504 (GB)	formosa	Ecuador
47	Hitchcock 21891 (US)	formosa	Ecuador
48	Penland & Summers 142 (US)	formosa	Ecuador
49	Gutierrez 2687 (COL)	candida	Ecuador
50	Mexia 6855 (US)	formosa	Ecuador
51	Asplund 9122 (S)	formosa	Ecuador
52	Asplund 19120 (S)	formosa	Ecuador
53	Harling & Andersson 11682 (GB)	candida	Ecuador
54	Harling & Andersson 11719A (GB)	formosa	Ecuador
55	Plowman & Kennedy 5811 (GH)	ulei	Peru
56	Idrobo & Schultes 1208 (US)	candida	Colombia
57	Plowman et al. 6724 (F)	candida	Peru
58	Schunke 3856 (F)	formosa	Peru
59	Von Sneidern s. n. (S)	formosa	Colombia
60	Lozano 594 (COL)	formosa	Colombia
61	Revilla 990 (MO)	formosa	Peru
62	De Jussieu s. n.	ulei	Peru
63	Huashikat 164 (MO)	candida	Peru
64	Ducke 12162 (GOEL)	cyaneosperma	Brazil
65	Woytkowski 5830 (F)	cyaneosperma	Peru

Table A.3--continued.

NO.	COLLECTION AND HERBARIUM	SPECIES	ORIGIN
66	Cardenas 1553A (NY)	cyaneosperma	Bolivia
67	Cardenas 1179 (NY)	cyaneosperma	Bolivia
68	Krukoff 5573 (NY)	cyaneosperma	Brazil
69	Nelson 33-301 (MO)	cyaneosperma	Bolivia
70	Killip s. n. (COL)	formosa	Colombia
71	Bonpland s. n. (?)	bonplandii	Colombia
72	Goudot s. n. (?)	bonplandii	Colombia
73	Pennell et al. 8604 (US)	bonplandii	Colombia
74	Uribe 4218 (COL)	bonplandii	Colombia
75	Schunke 9675 (F)	formosa	Peru
76	Williams 7748 (F)	formosa	Peru
77	Ancuash 161 (MO)	formosa	Peru
78	Killip & Smith 27656 (US)	ulei	Peru
79	Seibert 2145 (US)	cyaneosperma	Peru
80	Killip et al. 29227 (US)	ulei	Peru
81	Schunke 14157 (FLAS)	formosa	Peru
82	Schunke 14155B (FLAS)	candida	Peru
83	Meerow 1143 (FLAS)	plicata subsp. brevidentata	Bolivia
84	Schunke 14174 (FLAS)	formosa	Peru
85	Cabrera 3336 (COL)	formosa	Colombia
86	Schultes & Black 8478 (US)	candida	Colombia
87	Meerow 1108 (FLAS)	bakeriana	Peru

Table A.4. Data matrix for multivariate analysis of androecial characters of Amazonian Eucharis.

OTU	CHARACTER							
	1	2	3	4	5	6	7	8
1	5.7	2.7	6.0	10.0	16.2	1	1	1
2	6.2	2.2	5.0	11.6	16.8	1	1	1
3	5.8	2.5	5.6	16.0	19.0	1	2	1
4	6.5	2.5	6.5	12.5	21.0	2	1	1
5	4.9	2.2	6.3	13.5	23.0	1	2	1
6	3.5	1.5	4.7	16.8	09.0	2	1	1
7	3.7	1.2	3.5	11.3	10.0	3	2	1
8	4.0	1.2	3.5	10.0	15.0	3	2	1
9	3.5	1.3	5.4	10.0	14.5	1	2	2
10	4.5	2.0	5.2	10.0	15.5	1	2	1
11	4.0	1.5	4.0	10.0	15.0	1	3	1
12	4.7	2.7	6.7	09.0	17.5	1	2	1
13	5.0	2.5	7.5	08.5	21.0	2	2	1
14	4.2	1.7	4.8	17.2	19.3	2	3	1
15	4.0	2.5	7.0	12.8	22.5	2	1	1
16	6.4	1.0	2.6	07.6	09.4	1	2	1
17	5.2	2.0	6.2	10.5	14.2	1	3	1
18	2.8	1.8	3.8	08.0	10.0	2	1	2
19	1.8	1.5	4.0	06.0	09.3	2	1	2
20	1.7	0.9	2.0	05.8	06.4	2	1	1
21	4.0	1.5	5.0	08.0	12.0	2	1	1
22	1.2	1.0	3.7	08.5	10.2	2	2	2

Table A.4--continued.

OTU	CHARACTER							
	1	2	3	4	5	6	7	8
23	2.5	1.2	3.0	05.0	09.0	2	1	1
24	2.5	1.5	3.8	07.0	10.6	2	1	2
25	1.5	1.0	2.7	05.5	07.0	2	1	1
26	2.2	1.6	4.0	05.0	12.0	2	2	2
27	2.0	1.8	4.0	07.0	11.5	2	2	2
28	3.0	1.9	3.5	10.5	12.0	2	2	4
29	5.0	2.0	4.5	12.7	14.7	2	2	3
30	2.8	1.0	4.3	10.0	12.5	2	1	1
31	4.3	1.8	5.0	14.0	14.3	2	2	1
32	2.7	1.5	3.5	10.7	12.8	3	3	1
33	5.7	1.5	5.4	11.5	16.5	3	1	1
34	6.1	1.5	5.8	12.0	20.0	2	1	1
35	5.5	1.7	4.5	14.3	15.5	1	2	1
36	5.8	1.8	3.7	10.0	12.5	1	1	1
37	5.7	1.8	4.2	10.0	13.0	1	2	1
38	5.0	1.3	3.5	10.5	11.6	1	2	1
39	6.0	1.8	4.0	10.8	14.0	1	1	1
40	6.0	1.5	4.0	10.6	11.0	1	1	1
41	4.8	1.5	5.0	09.0	15.5	1	1	1
42	4.7	1.3	5.0	09.5	11.3	1	2	1
43	3.5	1.5	4.0	10.5	13.0	1	3	1
44	6.2	2.0	6.2	13.0	22.0	4	2	0



Table A.4--continued.

OTU	CHARACTER							
	1	2	3	4	5	6	7	8
45	6.0	2.5	6.0	09.5	14.0	5	2	0
46	7.4	2.2	4.5	08.2	16.0	5	2	0
47	6.0	3.0	6.5	10.0	18.5	3	3	1
48	4.0	2.0	6.0	13.8	20.0	5	3	0
49	4.6	2.0	4.3	07.0	13.5	5	3	0
50	5.1	2.5	7.3	09.0	20.0	5	3	0
51	5.2	2.5	5.8	10.2	22.5	5	2	0
52	5.6	2.6	7.0	11.6	18.6	5	2	0
53	3.5	1.7	3.8	11.0	17.2	3	2	1
54	6.0	2.0	6.0	13.8	18.2	5	2	0
55	4.5	1.5	5.2	12.0	17.0	5	2	0
56	4.7	1.9	4.3	11.2	14.0	3	3	1
57	5.3	1.8	4.5	10.0	20.0	5	3	0
58	4.0	2.0	7.1	12.2	20.0	5	3	0
59	5.5	2.0	4.0	10.0	15.2	5	2	0
60	5.9	2.8	4.5	08.0	17.0	5	3	0
61	5.4	2.5	5.6	10.6	18.5	5	2	0
62	5.0	1.7	4.4	12.4	15.5	5	2	0
63	5.5	2.2	5.0	09.5	16.0	5	2	0
64	4.5	1.6	3.7	09.5	13.3	4	2	1
65	3.5	1.5	3.5	11.0	12.0	4	2	1
66	5.0	2.0	5.0	09.0	17.0	4	3	1

Table A.4--continued.

OTU	CHARACTER							
	1	2	3	4	5	6	7	8
67	3.7	1.5	3.5	10.0	10.0	4	2	1
68	6.0	1.5	3.5	07.5	08.0	4	2	1
69	3.7	1.5	3.5	11.0	13.0	4	1	1
70	4.3	1.5	5.9	17.0	18.2	3	1	1
71	4.0	1.5	4.5	08.5	10.0	3	1	1
72	3.5	1.4	3.5	09.0	11.5	1	2	1
73	5.8	2.0	4.4	14.3	13.0	1	2	1
74	5.5	1.5	3.6	10.0	11.7	1	2	1
75	4.7	1.8	5.5	14.0	20.0	2	1	1
76	4.0	1.5	4.4	11.4	19.0	2	1	1
77	4.3	2.5	4.9	12.5	18.2	2	1	1
78	6.9	1.8	4.9	09.5	16.5	2	1	1
79	6.1	1.5	4.5	10.6	11.7	2	1	1
80	5.5	1.5	4.5	10.5	16.0	2	1	1
81	4.5	1.8	5.0	08.5	13.0	5	3	0
82	4.0	2.0	5.0	11.0	13.0	5	3	0
83	3.5	1.5	6.0	08.0	11.0	2	1	2
84	6.5	1.8	5.7	14.0	18.0	1	3	1
85	5.0	2.1	6.0	08.5	16.2	1	3	1
86	5.7	1.5	6.0	10.0	20.0	5	3	0
87	3.0	1.7	6.4	16.0	13.0	1	1	2

Table A.5. Operational taxonomic units (OTU's) for multivariate analysis of the Eucharis candida/formosa complex in eastern Ecuador.

NO.	COLLECTION AND HERBARIUM	SPECIES
1	Harling & Andersson 12915 (GB)	formosa
2	Harling et al. 7673 (GB)	formosa
3	Holguer 1504 (GB)	formosa
4	Hitchcock 21891 (US)	formosa
5	Penland & Summers 142 (US)	formosa
6	Gutierrez 2687 (COL)	candida
7	Mexia 6855 (US)	formosa
8	Asplund 9122 (S)	formosa
9	Asplund 19120 (S)	formosa
10	Harling & Andersson 11682 (GB)	candida
11	Harling & Andersson 11719A (GB)	formosa
12	Harling et al. 7201 (GB)	formosa
13	Harling & Andersson 17374 (GB)	formosa
14	Dodson 6636 (SEL)	formosa
15	Holguer 2655 (GB)	formosa
16	Asplund 9488 (S)	formosa
17	Harling 7400 (GB)	candida
18	Besse et al. 1598 (SEL)	candida
19	Besse et al. 1643 (SEL)	candida
20	Asplund 8853 (S)	candida

Table A.5--continued.

NO.	COLLECTION AND HERBARIUM	SPECIES
21	Besse et al. 1558 (SEL)	candida
		X formosa
22	Besse et al. 1563 (SEL)	candida
		X formosa
23	Holguer 3532 (GB)	formosa
24	Holguer 2960 (GB)	formosa
25	Prescott 438 (NY)	formosa
26	Asplund 19571 (S)	formosa
27	Benoist 4717 (P)	candida
28	Meerow 1103 (FLAS)	formosa

Table A.6. Data matrix for PCA and cluster analyses of the Eucharis candida/formosa complex in eastern Ecuador.

		CHARACTER																
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
OTU																		
1	10	65	6.2	2.0	6.2	45.0	10.8	40.0	39.0	17.0	20.0	13.0	22.0	4	2	0	5	
2	08	70	6.0	2.5	6.0	36.0	12.0	40.0	36.0	13.5	17.5	09.5	14.0	5	2	0	6	
3	10	60	7.4	2.2	4.5	42.0	11.0	28.5	25.2	10.6	13.2	08.2	16.0	5	2	0	2	
4	10	70	6.0	3.0	6.5	35.0	12.0	45.0	43.0	17.0	20.0	10.0	18.5	3	3	1	6	
5	05	70	4.0	2.0	6.0	42.0	11.0	45.6	38.7	15.4	20.5	13.8	20.0	5	3	0	4	
6	05	45	4.6	2.0	4.3	22.0	07.2	26.0	23.0	07.0	12.0	07.0	13.5	5	3	0	4	
7	06	60	5.1	2.5	7.3	39.0	10.0	33.8	30.0	10.0	17.0	09.0	20.0	5	3	0	6	
8	10	80	5.2	2.5	5.8	39.0	12.0	38.0	36.0	15.6	19.0	10.2	22.5	5	2	0	8	
9	04	59	5.6	2.6	7.0	33.0	10.5	30.0	29.0	13.0	15.0	11.6	18.6	5	2	0	5	
10	06	40	3.5	1.7	3.8	30.8	11.8	23.0	22.0	09.0	14.0	11.0	17.2	3	2	1	2	
11	10	58	6.0	2.0	6.0	44.5	11.0	26.0	25.0	12.0	16.2	13.8	18.2	5	2	0	6	
12	10	75	5.7	2.7	6.0	33.0	10.0	44.0	39.0	19.0	25.0	10.0	16.2	1	1	1	5	

Table A.6--continued.

		CHARACTER																
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
OTU																		
13	10	58	6.2	2.2	5.0	34.0	10.0	30.5	29.0	14.0	18.0	11.6	16.8	1	1	1	4	
14	06	65	5.8	2.5	5.6	35.0	10.0	40.8	36.0	13.0	16.0	16.0	19.0	1	2	1	5	
15	10	75	6.5	2.5	6.5	37.0	14.2	37.5	35.2	17.0	22.6	12.5	21.0	2	1	1	5	
16	10	75	4.9	2.2	6.3	40.0	10.0	42.0	40.0	15.5	21.0	13.5	23.0	1	2	1	5	
17	05	43	3.5	1.5	4.7	26.0	12.5	27.5	23.5	10.5	13.5	16.8	09.0	2	1	1	2	
18	07	50	3.7	1.2	3.5	30.0	07.5	26.5	26.0	11.0	13.0	11.3	10.0	3	2	1	6	
19	10	40	4.0	1.2	3.5	28.0	09.2	26.0	23.0	14.0	17.0	10.0	15.0	3	2	1	4	
20	10	46	3.5	1.3	5.4	28.5	07.3	20.7	20.5	14.4	13.4	10.0	14.5	1	2	2	5	
21	08	55	4.5	2.0	5.2	35.0	09.2	31.0	28.0	12.0	18.0	10.0	15.5	1	2	1	3	
22	08	55	4.0	1.5	4.0	31.0	07.8	32.0	30.0	13.0	17.0	10.0	15.0	1	3	1	6	
23	08	55	4.7	2.7	6.7	36.6	14.2	29.0	27.0	14.0	19.0	09.0	17.5	1	2	1	5	
24	10	60	6.0	2.5	7.5	34.0	09.4	27.6	25.0	13.5	16.5	08.5	21.0	2	2	1	5	



Table A.6--continued.

		CHARACTER																
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
OTU																		
25	10	70	4.2	1.7	4.8	30.0	12.0	43.3	40.0	12.0	15.5	17.2	19.3	2	3	1	5	
26	06	74	4.0	2.5	7.0	35.0	10.0	35.0	32.5	18.0	21.0	12.8	22.5	2	1	1	4	
27	08	40	6.4	1.0	2.6	30.0	04.6	07.5	11.5	25.0	23.0	07.6	09.4	1	2	1	4	
28	10	72	5.2	2.0	6.2	34.0	11.5	40.0	37.5	18.0	21.5	10.5	14.2	1	3	1	5	

Table A.7. Operational taxonomic units (OTU's) for multivariate analysis of the *Eucharis bouchei* complex. CR = Costa Rica, G = Guatemala, P = Panamá.

NO.	COLLECTION AND HERBARIUM	VARIETY	ORIGIN
1	Alston 8727 (BM)	dressleri	P, Coclé
2	Meerow 1107 (FLAS)	dressleri	P, Coclé
3	Wendland 207 (GOET)	darienensis	G
4	Sullivan 718 (MO)	darienensis	P, Darien
5	Folsom 4402 (MO)	darienensis	P, Darien
6	Folsom et al. 6582 (MO)	bouchei	P, Panama
7	Allen 5347 (US)	bouchei	CR
8	Kirkbride & Hayden 305 (MO)	bouchei	P, Panama
9	Witherspoon & Witherspoon 8372 (MO)	darienensis	P, Panama
10	Duke & Elias 3661 (GH)	darienensis	P, Darien
11	Gentry & Mori 13945 (MO)	darienensis	P, Darien
12	Stern et al. 499 (GH)	darienensis	P, Darien
13	Skutch 1585 (F)	bouchei	G
14	Seibert 466 (MO)	bouchei	P, Coclé
15	Lewis 2617 (MO)	bouchei	P, Coclé
16	Witherspoon & Witherspoon 8736	bouchei	P, Coclé
17	Allen 1228 (GH)	bouchei	P, Coclé
18	Mori & Kallunki 2014 (AAU)	bouchei	P, Colón
19	Mori et al. 6586 (AAU)	bouchei	P, Colón
20	Meerow 1158 (FLAS)	bouchei	P, Colón

Table A.8. Data matrix for PCA and cluster analyses of the Eucharis bouchei complex.

	CHARACTER																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
OTU																	
1	05	43	3.5	1.8	2.5	33.0	06.5	26.2	25.8	05.5	08.0	09.4	09.5	4	2	1	3
2	06	53	4.2	1.8	5.0	41.0	10.5	32.0	28.0	10.0	13.5	16.0	11.5	3	2	2	3
3	06	42	3.5	1.8	3.7	36.0	06.5	25.0	23.0	09.5	12.7	11.0	12.0	3	2	1	2
4	04	46	3.1	2.0	4.6	25.5	09.5	20.8	20.0	08.0	11.1	06.0	13.2	6	2	1	2
5	05	43	2.5	2.2	4.3	36.3	07.1	21.8	21.0	10.5	15.5	07.0	14.5	6	3	0	2
6	06	55	3.6	2.8	5.2	46.0	12.2	31.4	30.0	13.8	15.2	10.6	17.4	6	3	0	3
7	06	69	3.5	2.8	5.2	44.0	12.0	35.0	31.5	15.5	17.5	11.0	18.2	6	3	0	2
8	04	45	2.8	2.5	4.9	31.0	10.5	27.7	25.5	11.4	14.5	10.0	16.0	5	4	0	2
9	04	38	3.0	2.0	4.3	33.0	10.0	20.0	19.0	09.5	12.5	09.2	14.0	3	3	1	2
10	05	42	2.1	1.7	4.2	27.1	06.0	23.8	22.0	10.0	12.0	09.0	12.8	2	2	2	2
11	06	55	2.0	2.0	4.5	43.4	12.0	27.0	25.0	10.2	16.5	14.0	18.2	3	2	2	4
12	05	38	1.8	1.8	5.0	30.0	09.8	22.0	21.0	11.5	15.0	09.0	12.3	2	3	2	2

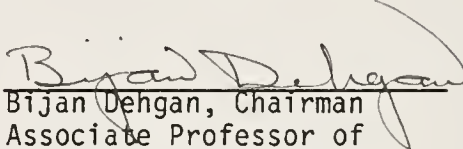
Table A.8--continued.

		CHARACTER																
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
OTU																		
13	04 41	5.0	5.1	5.1	5.1	35.0	10.5	24.2	21.1	09.8	14.5	12.0	15.4	4	3	0	2	
14	05 45	5.3	4.3	5.3	36.0	08.7	28.0	26.0	12.0	14.0	11.0	14.0	4	3	0	2		
15	07 50	6.9	5.0	6.9	43.7	10.8	26.8	25.0	14.0	14.6	16.7	16.0	4	3	0	2		
16	05 49	4.5	3.5	4.5	43.0	10.6	21.0	20.0	09.0	11.0	08.0	12.5	4	3	0	2		
17	03 50	6.5	4.7	6.5	45.0	12.0	23.5	22.0	11.5	15.5	12.8	14.5	4	3	0	2		
18	05 34	5.9	3.7	3.7	34.0	08.3	18.0	16.0	09.0	11.5	11.6	11.5	4	3	0	2		
19	05 35	3.7	4.0	4.0	33.0	07.0	21.6	19.5	08.0	10.0	10.0	12.4	4	2	0	2		
20	05 40	5.3	3.8	3.8	40.0	08.0	26.0	24.0	11.2	13.7	11.8	09.7	4	3	0	2		

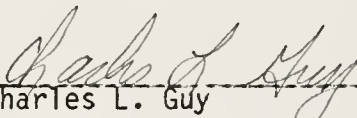
## BIOGRAPHICAL SKETCH

Alan W. Meerow was born on June 21, 1952, in Bronx, New York. He attended the State University of New York at Buffalo for one year. In California, a nascent interest in the plant sciences became fully developed, and led him back to school at the University of California, Davis. He graduated from UCD in 1978 with a B.S. degree in plant science (environmental horticulture and botany). After working for two years as botanical garden horticulturist, he began graduate studies at the University of Florida in horticultural plant systematics. Studies preliminary to this present work were completed in 1983 for the degree of Master of Science. He has been honored with grants and scholarships during his graduate career by the National Science Foundation, the Garden Club of America, the Florida Federation of Garden Clubs, and the Garden Writers Association of America. In 1985, he received a Certificate of Presidential Recognition from President Criser of the University of Florida. He is married to the former Linda Lee Fisher, and the couple's first child is due in November, 1986. Meerow is an authority on Amaryllidaceae, and has travelled widely in South America collecting plants of this family. He is also a freelance writer, and enjoys reading, gardening, and travelling in his spare time.

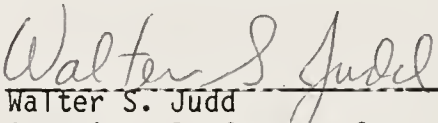
I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
Bijan Dehgan, Chairman  
Associate Professor of  
Horticultural Science


I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
Charles L. Guy  
Assistant Professor of  
Horticultural Science

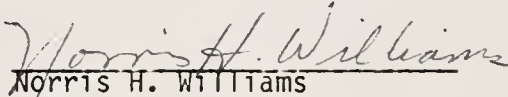
I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
Walter S. Judd  
Associate Professor of  
Botany

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
Thomas J. Sheehan  
Professor of Horticultural  
Science

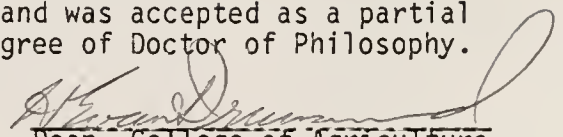
I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
Norris H. Williams  
Professor of Botany



This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School and was accepted as a partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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Dean, College of Agriculture

Dean, Graduate School -----

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